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CHANGES IN SPIDER COMMUNITY ATTRIBUTES ALONG A SUBALPINE  
SUCCESSIONAL GRADIENT

*Utah State University*

PH.D.

1979

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CHANGES IN SPIDER COMMUNITY ATTRIBUTES ALONG  
A SUBALPINE SUCCESSIONAL GRADIENT

by

Gerald Norman Waagen

A dissertation submitted in partial fulfillment  
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology  
(Ecology)

J. & Jessie E. Quinney  
Natural Resources  
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Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

1979

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Dr. W. E. Gertsch identified the spiders collected during the course of the study.

Gerald Norman Waagen

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## ABSTRACT

Changes in Spider Community Attributes  
Along a Subalpine Successional Gradient

by

Gerald Norman Waagen, Doctor of Philosophy

Utah State University, 1979

Major Professor: Dr. James A. MacMahon

Department: Biology

The spider communities of four stages of a successional sere leading to and including spruce forests were studied in northern Utah. Four seral stages were recognized. These include: meadows, aspen (Populus tremuloides) stands, subalpine fir (Abies lasiocarpa) forest, and the climax Engelmann spruce (Picea engelmannii) forests.

During the snow-free periods of 1976, 1977, and 1978, 15,987 spiders were collected by three methods including: pitfall traps, by beating vegetation, and with sweep-net samples. Additionally, 1600 15-second intervals of behavioral observations, and measurements of 182 web locations were made.

Of 99 species collected, 44 were considered residents of the sere; criteria for assigning the species to foraging strategies (3) and guilds (9) are presented. Five spider communities were ostensibly defined--one in the ground stratum of each of the stages and one in the tree stratum of the conifer stages.

The data were used to compare the guild strategies of the spiders of the seral stages and to address various hypotheses about successional

change in animal community characteristics. Increases with maturity as predicted were observed for 6 spider community parameters including: total biomass, species diversity--richness component, species diversity--equitability component, stratification and spatial heterogeneity, mean organism size, and temporal stratification. A life cycle hypothesis (i.e., short and simple life cycles in early stages, long and complex ones in mature stages) could not be tested because, depending on the life cycle type considered, I found diametrically opposed trends (semi-annual and biennial life cycle types both increased with maturity).

The spider species of the ground-stratum meadow community were primarily dispersed in a time dimension (seasonal); the spiders of the tree-stratum community were primarily distributed in a spatial dimension (microhabitat). Spiders of the forest ground-strata communities were dispersed in spatial and temporal dimensions. No dimension was ascertained to be of fundamental importance.

Distributions of ground-dwelling species with different foraging strategies, and the resident species of the ground-stratum communities were correlated canonically to 8 environmental variables. Spider species of the meadow community were correlated with a bare dirt variable. Spiders of the aspen community were correlated with 2 environmental variables including: grasses and forbs and a low foliage index. Hunting spiders were correlated with the meadow and aspen variables. Ambushing spiders, web-building spiders, and the spider species of the ground stratum spruce community were correlated with 5 environmental variables including: litter depth, canopy cover, tree basal area, dead leaves and needles, and logs.

## INTRODUCTION

Two basic problems in community ecology are how species in communities are organized spatially and temporally, and how the community organization changes in time (Post and Riechert, 1977). Important features influencing community organization are the physical characteristics of a habitat and the competitive relationships among the spatially coexisting species. Although it has often been demonstrated that the outcome of competition is influenced by environmental conditions (Gause, 1934; Nageli, 1865; Park, 1962), one can postulate that 2 differentiable processes are involved. Potential inhabitants must be capable of physically surviving at a site, and they must be competitively successful; the specific attributes of the component species must be ecologically complementary.

Spiders have several qualities which recommend them as subjects for studies in community ecology. They are widely distributed, numerically abundant, and ecologically important as predators (Moulder and Reichle, 1972; Riechert, 1974; Robinson and Robinson, 1970). As a group they are biologically quite homogeneous, being small, soft-bodied, euryphagous carnivores which use silk and/or venom to subdue their prey (Enders, 1973). Physical parameters which have been implicated in a causal fashion with the distribution and abundance of spiders include: support flexibility (Enders, 1973), inter-support distance (Cherrett, 1964), and degree of protection from wind (Duffey, 1962) for orb-web weavers; light intensity (van der Aart, 1973), type of substrate (Lowrie, 1973), and orientation of the

vegetation (Greenquist and Rovner, 1976) for lycosids; humidity and slope of soil (Coyle, 1971) for antrodiaetids; and substrate architecture (Hatley, 1978; Robinson, 1978) for the shrub stratum spiders of a community. Interpretation of the relationships between changes in the environment and those in the spider populations is facilitated by the fact that spiders are fairly independent of a given species of vegetation or prey. Their occurrence is primarily determined by the physical factors of the environment (Elliott, 1930; Huhta, 1971; Lowrie, 1948).

The nature of the interactions between coexisting spider species can be inferred if the manner in which the resources of the habitat are partitioned is known. Spider species may be active at different seasons (Dondale, 1961; 1977; Smith, 1928), and during different parts of the day (Dondale et al., 1972; Gertsch and Riechert, 1976). In addition they may differ in size (Uetz, 1977), foraging technique (Turnbull, 1973), and microhabitat preference (Colebourn, 1974; Gertsch and Riechert, 1976; Luczak, 1963; Nyffeler and Benz, 1978). Segregation of spider species along these axes presumably results in differential exploitation of the prey resources of a habitat.

The responses of individual species to environmental variables create the context within which a community is organized. A description of the pattern of occurrence in time and space together with the "important" ecological attributes (i.e., size and foraging strategies, for spiders) of the component species populations of a community represents the community structure. Most previous workers who have described the structure of spider communities have emphasized

either the space (Post and Riechert, 1977) or time dimensions (Barnes and Barnes, 1955; Muma, 1973), and deduced the nature of interactions from such incomplete information. But, if adequate empirical data pertaining to both the spatial and temporal dynamics of a community are not available, the description of that community's structure is necessarily incomplete.

The question of how the organization of a community changes in time, at one scale, can be approached by studying the patterns of change among habitats which are presumed to represent a successional chronosequence. There have been numerous studies of ecological succession in spider communities (Barnes, 1953; Berry, 1967; Duffey, 1978; Huhta, 1971; Leitinger-Mikoletsky, 1940; Lowrie, 1948; Martin, 1965). The 13 year study by Huhta is the only one in which a single site was investigated over a long period. Using quadrats and pitfall traps, Huhta studied the succession of spider communities on the floor of a European spruce forest, parts of which had been burned and/or clear-cut. After burning, the species composition changed radically for 2 years; maximum divergence was reached after 7 years when 70% of the spiders were those typical of pioneer or early developmental stages. Thirteen years after burning, the composition of the spider community was similar to that found in a climax stand. Species diversity (Fisher's  $\alpha$  index) declined to a minimum at 2 years, then increased to a maximum at 7 years, and returned to the pre-burning value after 13 years. An index of similarity (Kendall's  $\tau$  Coefficient) comparing the burned to the original community declined for the first 7 years, after which it increased, coinciding with the pattern of change of the ecological spectrum of the spiders (i.e., xeric-adapted



vs. mesic-adapted species). Huhta noted that, "The succession in the spider community did not bear any relation to the course of the botanical succession after burning-over," but rather that, "...the spider succession showed an obvious parallellism with the general physiognomic development of the habitat."

Leitinger-Mikoletsky (1940) concluded that successional changes in the spider fauna of a spruce sere reflected physiognomic changes of the vegetation. Three phases were recognized. Wandering spiders are associated with clear-cut fields, whereas after the field is well-vegetated, web-spiders are included in the community. Web-spiders eventually predominate in mature closed-canopy stands.

Lowrie (1948) collected spiders from lake shore through beech-maple forest stages of a sere bordering Lake Michigan. He termed the first stage the "lycosid associates." Salticids and thomisids were abundant in the thickets of the middle developmental stages and linyphiids predominated in the climax forest, which contained the greatest number of species for which only a single specimen was collected. Species richness peaked in the late-developmental black oak stage. Characteristic spider species were present in each of 3 stages of log decay in the climax forest. An intact log had a fauna of pioneer, vagrant spiders, while agelenids, amaurobiids, and some theridiids built webs in the crevices and cavities which became available as decay proceeded. As termination was approached the log was again populated by vagrant spiders which ran about on the "crumbling mass".

Barnes (1953) recognized 9 seral communities between intertidal marsh grass and a climax live oak forest along the eastern coast

of North Carolina. Although he did not examine the climax forest, he asserted that each habitat type had a distinct assemblage of spider species, constant over space, and exhibiting no significant seasonal changes. He termed this assemblage an "abstract community." Observed differences from the ideal structure were attributed to zoogeographic and experimental sampling error. Lycosids were most abundant in the late developmental stages, and maximum spider density and species richness occurred in the most mature community studied.

Martin (1965) found that the web-spider families Linyphiidae, Hahniidae, and Theridiidae predominated in the older stands of a red pine plantation in central Ontario, whereas the younger trees harbored more species of Lycosidae and Gnaphosidae.

Berry (1967) studied old-field succession in the Piedmont region of North Carolina. He concluded that old-field species assemblages differed from those of the forest, although he did not specify the nature of the difference. The greatest abundances of spiders were found in early developmental stages.

In the most recent publication ostensibly pertaining to ecological strategies of spiders in pioneer and mature habitats, Duffey (1978) reached the conclusion that,

"...easily acquired components of habitat description, especially structure, floristics, history, management, area and climatic features, are important factors in understanding faunal succession and the occurrence and status of a species in a particular locality."

None of the above was presented or discussed.

## METHODS

### The Study Area

The sere examined is one of several found in the Central Rocky Mountains. Subalpine meadows are succeeded by ecosystems dominated by aspen (Populus tremuloides) and in turn by subalpine fir (Abies lasiocarpa). The climax forest is dominated by Engelmann spruce (Picea engelmannii).

"The study site was located in the Wasatch Mountains of northern Utah, principally in or adjacent to the Utah State University School Forest, Cache County and Rich County, Utah (elevation = 2,470 m). In this area, aspen typically forms narrow bands 20-40 m wide around the periphery of small meadows (0.3-10 ha, rarely larger). Larger expanses of subalpine fir-dominated forest grade into climax spruce-dominated forest. These seral stages form a mosaic with stages from other seres, notably lodgepole pine (Pinus contorta) after fire. Clumps of subalpine fir are commonly found in the interiors of meadows, and individuals or small groups of aspen, or even small openings which might be considered "meadow", can be found within fir and spruce forest. Thus, in each of the seral stages examined, vegetative components from adjacent stages probably exert some influence on the (animals) present.

"The School forest has been subject to light to moderate grazing by both sheep and cattle for (at least) several decades. While meadows were probably severely overgrazed in the early 1900's, (I) assume that current meadow and forest conditions reflect those which would be present and affecting (animals) under pristine conditions...." (Andersen et al., 1979).

With respect to the type of vegetation present, Schimpf et al. (1979) noted, "the life-form composition of the vegetation is rather simple, consisting of herbs and, except in the meadow, trees. Individuals of shrubby species are uncommon...."

### Sampling plots

Three replicate plots each 0.1 ha in size (20m by 50m) were

surveyed and staked in each seral stage (M = meadow, A = aspen, F = fir, S = spruce; Figs. 1 and 2). Two plots in each stage (M1, M2, A1, A2, F1, F2, S2, S3) were considered representative of the stage indicated. One plot of each stage was chosen with the intention of sampling the spiders from plots approximating the extreme habitats present in the sere. Thus, M3 and A3 were relatively well-vegetated plots on steep, moist, east-facing slopes. Plot F1, though dominated by spruce (see Appendix) was physiognomically like the representative fir plots, F1 and F2; F3 was a spruce-like plot dominated by fir trees. (The terms "representative" and "spruce-like" are subjective terms referring to my Gestalt impressions of the habitats.)

#### The collecting techniques

A central line of 5 pitfall traps was installed within each plot and used to sample spiders of the litter and ground strata (together hereafter referred to as "ground stratum"). The traps used were a smaller version (8 cm wide, 10 cm deep) of the trap described by Uetz and Unzicker (1976); a plywood roof (Fig. 3) was used instead of the wire grill suggested.

The above-ground strata were sampled each week on clear (i.e., no clouds were visible), calm (i.e., no discernible wind) days, between 1500 hr and 1800 hr. Branches of the "tree stratum" (15 cm to 2 m ht) were sampled with a beating cloth and stick. Because of the destructive nature of the technique, a group of branches was sampled only once a season.

The herbaceous stratum was sampled with a sweep net. There were so few non-meadow herbaceous-layer spiders (less than one spider/hr of

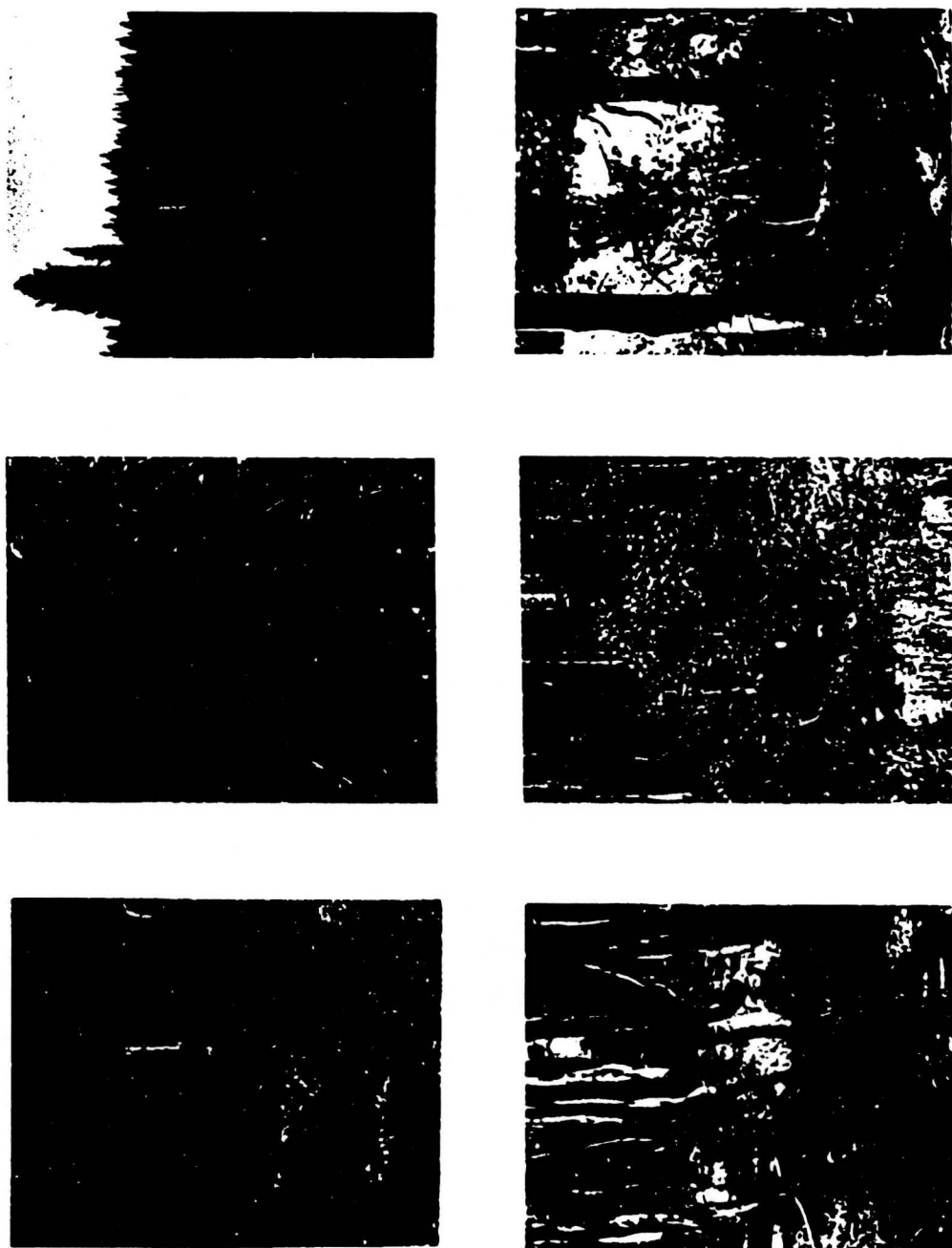


Figure 1. Meadow and aspen plots, 10 July 1979; left to right, top: M1, M2, M3; bottom: A1, A2, A3. 8



Figure 2. Fir and spruce plots, 10 July 1979; left to right, top: F1, F2, F3; bottom: S1, S2, S3.



Figure 3. Middle pitfall trap in M2, 10 July 1979.

sampling effort in 1977) that only the meadow herbs were sampled in 1978. Fifty standard sweeps (Whittaker, 1952) were repeated 3 times and all spiders collected were pooled as a sample unit. The sweep net was emptied after 25 sweeps if so much vegetation was swept into the net that sampling efficiency seemed to be impaired.

Two non-systematic sampling procedures were used. I located as many webs as possible of each species of web-spider, and for each web I measured height above ground and size (length of line-web, diameter of sheet-, orb-, space-, or surface-covering-web). The relation of the web to the trunk of the tree and the peripheral branches, and the form of a retreat, if present, were described. The inhabitant was collected, measured, and identified.

To evaluate the time-budgets of diurnal hunting spiders, whenever I sighted an individual which was foraging, I recorded total distance moved, microhabitat occupied (Table 8), and height above the surface if applicable, at 15-sec intervals. An individual spider was generally observed for 25 intervals (375 secs). The temperature of the surface upon which the spider was foraging most of the time was measured and recorded. The spider was collected if possible.

#### Evaluation of the sampling methods

The use of sweep nets, beating cloths, vacuum devices, quadrats and Tullgren funnels does not provide satisfactory estimates of spider density. Different collectors or even the same individual at different times may use the above devices in different ways producing various errors (Turnbull, 1973). Turnbull also noted that the sweep net is totally useless for some species.



Gray and Treloar (1933) concluded that the number of sweeps which would be required to achieve, "even a 50% error range...is so large as to preclude the usefulness of the technique...." Based on sweep net samples, Muma and Muma (1949) concluded that oxyopids are nocturnal hunters; whereas Comstock (1912), Gertsch (1949), Vollmer and MacMahon (1974), and Lowrie (1942, 1948, 1971) classify oxyopids as diurnal hunters. During the night, oxyopids are suspended motionless from a single strand of webbing and they are readily captured by sweeping. During the day they are active and alert, and fewer specimens are captured (Lowrie, 1971). If the time of activity of a species is to be determined, some method other than sweeping, beating, or vacuuming is probably preferable. Luczak (1959), however, considers the sweep net to be an accurate non-selective sampling tool.

The relative abundance of spiders captured in pitfall traps may be biased for the following reasons: 1) the likelihood of capture is greater for more active spiders (Heydemann, 1961; Turnbull, 1973; Huhta, 1971); 2) the preservative or the microhabitat associated with the trap (Fig. 3) may be attractive or repellant to different individuals (Turnbull, 1973); 3) in some habitats movement may be impeded (Heydemann, 1961); 4) climate may unpredictably influence the number of individuals captured (Greenslade, 1964; Southwood, 1966).

Huhta (1971) realized the problems associated with interpretation of data from pitfall collections but used this technique because, "...it is useful for comparing numbers of a given species over a range of habitats," and, "epigeic spiders, because of their great size and activity, possess a greater importance in the community than suggested by their number per unit area."

Breymeyer (1966), Heydemann (1961) and Uetz (cited in Uetz and Unzicker, 1976) refer to "penetrance" or "active density" rather than abundance of spiders in pitfall traps, and make no pretense that absolute density is being measured.

When sampling accuracy of pitfall traps was compared to a density-estimating technique of known reliability, Uetz and Unzicker (1976) concluded that pitfall traps, "can be used, with caution, in ecological studies." The conditions which they considered necessary include: cursorial spiders sampled; long collection periods; comparison of simultaneous collections; habitat impedance considered; data supplemented by a second method; and known sources of error reduced. These conditions were not in the present study.

#### Identification and measurement of specimens

All specimens were preserved and stored in 70% ethanol. They were identified to species or assigned to OTU's (Vandermeer, 1972). Body length (B.L.) was measured to the nearest 0.1 mm using a micro-ruler.

#### Schedule

The study was begun in 1976. June and July of that year were devoted to preliminary reconnaissance. Plots were selected and pitfall traps were installed on 23 July. The number of trap-hours per week was the same during 1977 and 1978, with the exception of the addition of a third fir plot (F3) during the latter year. The last snow-free day for 1977 and 1978 was 5 November, on which date all pitfall traps were emptied.

### Environmental parameters

Values for 9 environmental parameters were obtained between 24 August and 9 September 1978, in each of the 12 plots. High ( $15 \text{ cm} < \text{ht} < 2 \text{ m}$ ) and low ( $\text{ht} < 15 \text{ cm}$ ) foliage density indices were derived using the pole-tangent method (Landres and MacMahon, 1980). Two 50 m transects, 10 m apart, were run, equidistant from the edge and the center of each rectangular plot. Tree basal area values were calculated by summing the cross sectional areas (diameter-breast-high was measured) of each tree in a plot. A canopy cover index was the number of squares obscured in the 6 x 6 grid of the viewfinder of a single-lens reflex camera with a normal ( $45^\circ$  subtended) lens, divided by the total number of squares (180). The camera was placed directly over each pitfall trap in a plot.

Percent of surface area covered by grasses and forbs, dead leaves and needles, bare ground, and logs were estimated as the average values obtained in 10 randomly selected areas within each plot measured using a standard Daubenmire frame (10x50 cm) (Daubenmire, 1956). Litter depth values are the averages of 20 measurements 0.2 m in the cardinal directions from each of the 5 pitfall traps.

### Analytical techniques

Cluster analysis was used to ordinate the plots. A program (CLUSTAR) designed by H. Charles Romesburg and written by Kim Marshall was used for the cluster analysis. Samples (each plot-year) were compared by the Bray-Curtis Similarity Coefficient. Objects of the samples were species and families of spiders; attributes were the number of individuals per object. Denrograms were generated from the resemblance matrices by using the UPGMA clustering method (unweighted pair-group method using arithmetic averages).

Relative abundances of spider groups of the plots were related to 9 environmental variables by canonical correlation analysis (CCA, Morrison, 1967). There were 12 samples (plots); the maximum number of variables which could be analyzed at one time was 11, since more samples than variables is a requirement of the technique.

CCA had 2 significant limitations (Gauch and Wentworth, 1978): 1) it is assumed that the variables are linear; 2) if singularity (values of a subset of variables sums to 1.0) is present in the data it will not be analyzed. The latter limitation has the practical effect of further limiting the number of variables which can be compared. A rough assessment of the linearity of the variables was sufficient to determine that the first assumption was violated.

However, van der Aart and Smeenk-Enserinck (1976) used CCA to compare the distributions of a set of hunting spiders to a set of environmental variables and concluded that the technique was of value. It may be that the simple physical indices used as environmental variables in that study (and in the present one) are correlated in a unique fashion to spider distribution, so that it seems to work very well for spiders and their physical environments.

#### Terminology

A resident species is defined as one for which at least one adult was collected during 2 of the 3 field seasons and for which at least 5 individuals were collected during the 3 seasons.

An accidental species (Futuyma and Gould, 1979; MacMahon and Trigg, 1972) is a resident in the series, but has less than 5% of its

total number in the particular seral community being considered, in which it is "accidental."

An incidental species (Janzen, 1977) is one which is not resident in any community of the sere studied. Individuals which have dispersed from a distant (not defined) habitat are incidental.

## RESULTS

Between 23 July 1976 and 5 November 1978 I collected 15,987 spiders, belonging to 97 species in 16 families and 9 guilds (Tables 1, 2, 3, 4; Figs. 4, 5). Fifty-one of the species were considered incidental to the sere. The 44 species considered resident (Table 4) were distributed among the ground strata of all 4 seral stages and the tree strata of the fir and spruce stages. There were no resident spider species in the herbaceous strata of the sere, or the tree stratum of the aspen stages. Therefore, I ignore the 202 herbaceous layer specimens collected over the 3 years, as well as the 32 aspen tree specimens (Table 2).

Plot ordination and definition of communities of the sere

It was presumed that 6 communities were present, a ground stratum community in each stage and tree strata communities in the fir- and spruce-dominated stages. Rather than arbitrarily defining the communities, spider taxa were used as the variables to ordinate the plots in relation to each other.

The relative abundances of ground strata spider families during each year for each plot (28 samples) were compared by cluster analysis (Fig. 6). The least similarity (0.38) is between meadow and forest samples. Samples from "typical" spruce stands form a discrete group (coefficient of similarity = 0.45) within the forest sample. The coefficient of similarity of a cluster of 5 aspen samples with a large heterogeneous assemblage of forest samples is 0.61. At a similarity coefficient value of 0.65 there are 4 clusters which correspond to meadow, spruce, aspen, and a fir, aspen, fir-like spruce (S1) cluster, if the 1976 samples are excluded. The similarity index used (Bray-Curtis Similarity Coefficient, Bray and Curtis, 1975) included quantitative and qualitative differences among the

Table 1. Species list, spiders of a spruce-fir sere.

<u>Taxon</u>	<u>Status</u>
<b>Agelenidae</b>	
<u>Circurina robusta</u>	Resident
<b>Amaurobiidae</b>	
<u>Callobius nomeus</u>	Resident
<b>Antrodiaetidae</b>	
<u>Antrodiaetus montanus</u>	Resident
<b>Araneidae</b>	
<u>Aculepeira packardii</u>	Incidental
<u>Araneus nordmanni</u>	Resident
<u>Araniella displicata</u>	Resident
<u>Erigone dentosa</u>	Incidental
<b>Clubionidae</b>	
<u>Castianeira occidentis</u>	Incidental
<u>Micaria "A"</u>	Resident
<u>Micaria "B"</u>	Resident
<u>Micaria "C"</u>	Incidental
<u>Micaria "D"</u>	Incidental
<u>Scotinella pelvicolens</u>	Resident
<b>Dictynidae</b>	
<u>Dictyna brevitarsus</u>	Resident
<u>Mallos trivittatus</u>	Resident
<b>Erigonidae</b>	
<u>"M1"</u>	Resident

Table 1. Continued

<u>Taxon</u>	<u>Status</u>
<b>Erigonidae (continued)</b>	
"M2"	Resident
"M3"	Resident
"M4"	Resident
"M5"	Resident
"M6"	Resident
"M8"	Resident
11 unidentified erigonids	Incidental
<b>Gnaphosidae</b>	
<u>Drassylus lamprus</u>	Resident
<u>Gnaphosa muscorum</u>	Resident
<u>Haplodrassus eunis</u>	Resident
<u>Orodassus coloradensis</u>	Resident
<u>Zelotes tuobus</u>	Resident
<b>Hahnidae</b>	
<u>Neoantistea</u> sp.	Incidental
<b>Linyphiidae</b>	
<u>Anacornis proceps</u>	Resident
<u>Bathyphantes</u> sp.	Resident
<u>Cerogonol bicornis</u>	Resident
<u>Helophora tunagyna</u>	Resident
<u>Lepthyphantes arborea</u>	Resident
L. "B"	Resident



Table 1. Continued

<u>Taxon</u>	<u>Status</u>
<u>Linyphiidae (continued)</u>	
<u>L. calcarata</u>	Incidental
<u>L. pollicaris</u>	Incidental
<u>L. ranieri</u>	Incidental
6 unidentified <u>leptyphantes</u> spp.	Incidental
<u>Pityohyphantes cristatus</u>	Resident
<u>Wubana reminescens</u>	Resident
<u>Zornella cultrigera</u>	Incidental
12 unidentified linyphiids	Incidental
<u>Lycosidae</u>	
<u>Alopecosa kochi</u>	Resident
<u>Arctosa aloigena</u>	Resident
<u>Pardosa mackenziana</u>	Resident
<u>P. sternalis</u>	Incidental
<u>P. wyuta</u>	Resident
<u>Schizocosa mccooki</u>	Incidental
<u>Oxyopidae</u>	
<u>Oxyopes</u> sp.	Incidental
<u>Philodromidae</u>	
<u>Philodromus alascensis</u>	Resident
<u>P. rufus</u>	Resident
<u>Thanatus formicinus</u>	Incidental

Table 1. Continued

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Philodromidae (continued)	
<u>Tibellus oblongus</u>	Incidental
Salticidae	
<u>Pellenes americanus</u>	Resident
<u>P. laggani</u>	Incidental
<u>Phidippus borealis</u>	Incidental
<u>Metaphidippus aeneolus</u>	Resident
<u>Sitticus finschi</u>	Incidental
<u>Talavera minuta</u>	Resident
"S8"	Incidental
Theridiidae	
<u>Dipoena tibialis</u>	Resident
<u>Steatoda hespera</u>	Resident
<u>Theridion montanus</u>	Resident
<u>T. neomexicanus</u>	Incidental
<u>T. ohlerti</u>	Resident
<u>T. rabuni</u>	Incidental
Thomisidae	
<u>Misumenops varia</u>	Incidental
<u>Xysticus montanensis</u>	Incidental
<u>X. sp.</u>	Incidental
Incertae sedis	
3 unidentified species	Incidental

Table 2. Number of specimens collected.

	Ground	Herbaceous	Tree
<u>Meadow</u>			
1976	470	17	
1977	1005	35	
1978	<u>1411</u>	<u>8</u>	
	2886	60	
<u>Aspen</u>			
1976	303	0	9
1977	1785	54	23
1978	<u>2442</u>	<u>0</u>	<u>0</u>
	4530	54	32
<u>Fir</u>			
1976	146	12	56
1977	1102	65	568
1978	<u>1342</u>	<u>0</u>	<u>785</u>
	2590	77	1409
<u>Spruce</u>			
1976	290	2	8
1977	1265	9	620
1978	<u>1094</u>	<u>0</u>	<u>818</u>
	2649	11	1446
Total	12655	202	2887

Table 3. Three ecological strategies and 9 spider guilds. See discussion for criteria and justification for this schema.

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- I. Active Hunters
  - 1. Diurnal
  - 2. Nocturnal
- II. Ambushers
  - 3. Diurnal
  - 4. Nocturnal
- III. Web spiders
  - 5. Line-web
  - 6. Surface-covering-web (i.e., planar web covering a surface)
  - 7. Orb-web (i.e., planar vertical web)
  - 8. Sheet-web (i.e., planar horizontal web)
  - 9. Space-web (i.e., scatter line or 3-dimensional web)

Table 4. Attributes of the 44 resident spider species including: size; phenology; diel activity inferred from (n) time-partitioned pitfall-trap specimens. For guild designations see Table 3. N/A = not applicable.

Code	Taxon	Body Length in mm M: $\bar{x}$ (S.D.) F: $\bar{x}$ (S.D.)	Life Cycle	Breeding Period	Daily (n) Activity	Guild (1-9)
F. Agelenidae						
E1	<u>Cicurina robusta</u>	5.17(0.47) 6.71(0.89)	annual	fall	0.93 nocturnal (75)	4
F. Amaurobiidae						
R1	<u>Callobius nomeus</u>	7.46(0.05) 9.33(1.09)	biannual	fall	0.85 nocturnal (258)	6
F. Antrodiaetidae						
N1	<u>Antrodiaetus montanus</u>	11.43(1.68)	biannual	fall	1.0 nocturnal (12)	4
F. Araneidae						
A1	<u>Araneus nordmanni</u>	6.03(0.72) 8.85(2.33)	biannual	fall	diurnal	7
A2	<u>Araniella displicata</u>	7.70	annual	spring	diurnal	7
F. Clubionidae						
C3	<u>Micaria "A"</u>	3.41(0.139) 3.84(0.41)	annual	summer	0.9 diurnal (137)	1
C4	<u>Micaria "B"</u>	3.31(0.77) 3.71(0.39)	annual	spring	0.79 diurnal (57)	1
C2	<u>Scotinella pelvicolens</u>	1.97(0.12) 2.42(0.97)	annual	summer	0.5 diurnal (14) <sup>a</sup>	1 <sup>1/2</sup>

Table 4. Continued

Code	Taxon	Body Length in mm M: $\bar{x}$ (S.D.) F: $\bar{x}$ (S.D.)		Life Cycle	Breeding Period	Daily (n) Activity	Guild (1-9)
F. Dictynidae							
D2	<u>Dictyna brevitarsus</u>	2.49(0.28)	2.62(0.22)	annual	spring	N/A	6
D3	<u>Mallos trivittatus</u>	4.00	5.88(0.73)	biannual	fall	N/A	5
F. Erigonidae							
M1		1.69(1.25)	1.60(0.12)	semi-annual	spr. & fall	N/A	8
M2		1.60(0.15)	1.96(0.24)	annual	spring	N/A	8
M3		1.43(0.22)	1.59(0.19)	annual	fall	N/A	8
M4		1.48(0.09)	1.62(0.15)	annual	fall	N/A	8
M5		1.66(0.97)	1.85(0.19)	biannual	spr. & fall	N/A	8
M6		1.48(0.09)	1.62(0.15)	annual	fall	N/A	8
M8		1.74(0.17)	1.77(0.18)	semi-annual	spr. & fall	N/A	8
F. Gnaphosidae							
G4	<u>Drassylus lamprus</u>	3.74(0.23)	4.04(0.41)	annual	spring	0.81 diurnal (43)	1
G3	<u>Gnaphosa muscorum</u>	7.11(1.11)	9.10(1.38)	biannual	summer	0.75 nocturnal (52)	4

Table 4. Continued

Code	Taxon	Body Length in mm M: $\bar{x}$ (S.D.) F: $\bar{x}$ (S.D.)		Life Cycle	Breeding Period	Daily (n) Activity	Guild (1-9)
F. Gnaphosidae (continued)							
G5	<u>Haplodrassus eunis</u>	4.06(0.29)	5.03(0.67)	annual	spring	0.5 nocturnal (14) <sup>b</sup>	2
G2	<u>Orodassus coloradensis</u>	8.28(0.72)	9.24(2.29)	biannual	fall	0.93 nocturnal (15)	4
G1	<u>Zelotes tuobus</u>	5.57(0.36)	6.28(0.75)	annual	summer	0.85 diurnal (420)	1
F. Linyphiidae							
K2	<u>Anacornis proceps</u>	2.15(0.17)	2.58(0.20)	annual	fall	N/A	8
J6	<u>Bathypantes</u> sp.	3.12(0.21)	2.95(0.41)	annual	spring	N/A	8
K1	<u>Coreogona bicornis</u>	2.28(0.11)	2.50(0.17)	annual	fall	N/A	8
J3	<u>Helophora tunagyna</u>	3.11(0.21)	3.67(0.30)	annual	fall	N/A	8
I7	<u>Lepthyphantes arborea</u>	2.28(0.23)	2.57(0.17)	annual	summer	N/A	8
I6	<u>Lepthyphantes</u> "B"	3.15(0.21)	2.87(0.26)	annual	spring	N/A	8
I1	<u>Pityohyphantes cristatus</u>	4.54(0.68)	5.00(0.45)	annual	spring	N/A	8
K3	<u>Wubana remescens</u>	2.36(0.20)	2.87(0.36)	annual	fall	N/A	8

Table 4. Continued

Code	Taxon	Body Length in mm M: $\bar{x}$ (S.D.) F: $\bar{x}$ (S.D.)		Life Cycle	Breeding Period	Daily(n) Activity	Guild (1-9)
F. Lycosidae							
L3	<u>Alopecosa kochi</u>	9.31(0.75)	10.36(1.50)	biannual	spr. & fall	0.68 diurnal (19) <sup>c</sup>	4
L1	<u>Arctosa alpigena</u>	5.99(0.44)	7.44(0.92)	annual	spring	0.73 nocturnal (79)	2
L2	<u>Pardosa mackenziana</u>	5.49(0.28)	6.43(0.70)	annual	spring	0.86 diurnal (615)	1
L5	<u>Pardosa wyuta</u>	6.12(0.54)	6.47(1.17)	annual	spr. & fall	diurnal (1)	1
F. Philodromidae							
P1	<u>Philodromus alascensis</u>	4.76(0.41)	5.50(0.72)	annual	spring	0.6 diurnal (10)	3
P2	<u>Philodromus rufus</u>	4.25(0.89)	4.27(0.44)	annual	spring	diurnal	3
F. Salticidae							
S2	<u>Metaphidippus aeneolus</u>	4.48(0.39)	4.67(0.15)	annual	spring	diurnal	1
S1	<u>Pellenes americanus</u>	4.98(0.26)	6.40(1.10)	annual	summer	diurnal	1
S5	<u>Pellenes laggani</u>	4.60(0.56)	5.70(0.42)	annual	summer	diurnal	1
S3	<u>Talavera minuta</u>	2.20(0.23)	2.79(0.25)	annual	spring	1.0 diurnal (2)	1



Table 4. Continued

Code	Taxon	Body Length in mm M: $\bar{x}$ (S.D.) F: $\bar{x}$ (S.D.)	Life Cycle	Breeding Period	Daily(n) Activity	Guild (1-9)
F. Theridiidae						
T2	<u>Dipodops tibialis</u>	1.84(0.10) 3.57(0.34)	annual	spring	N/A	9
T1	<u>Steatoda hespera</u>	4.35(0.63) 5.20(0.94)	annual	spring	N/A	9
T4	<u>Theridion montanus</u>	2.47(0.06) 3.40(0.35)	annual	spring	N/A	9
T3	<u>Theridion ohlerti</u>	2.16(0.23) 2.47(0.25)	annual	spring	N/A	9

<sup>a</sup> Phaneropterus is diurnal, Dondale et al., 1972.

<sup>b</sup> Haplodraeus is nocturnal, Post and Riechert, 1977.

<sup>c</sup> Alopecosa kochi is nocturnal in the fall. Hagstrum, 1970.

Figure 4. Relative abundances of spider families in 12 plots  
(1977 and 1978 samples pooled). Top, families included  
in upper 90%; bottom, families included in lower 10%.  
B = Philodromidae; C = Clubionidae; E = Agelenidae;  
G = Gnaphosidae; I = Linyphiidae; L = Lycosidae; M =  
Erigonidae; N = Antrodiaetidae; P = Thomisidae; R =  
Amaurobiidae; S = Salticidae; T = Theridiidae.

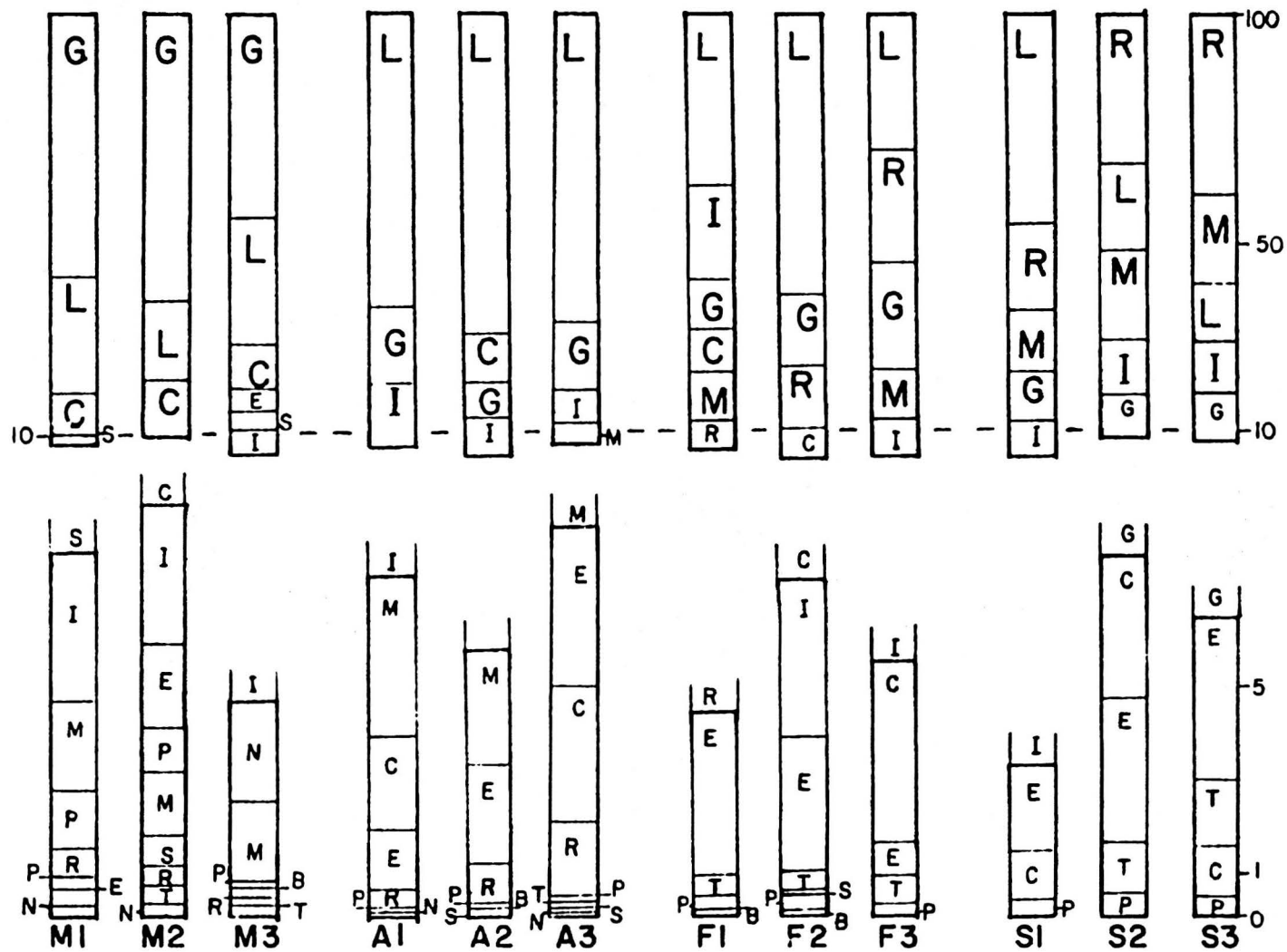


Fig. 5. Relative abundances of 6 spider guilds in 12 plots.

Guilds designated as follows: clear = diurnal hunter;  
stippled = nocturnal hunter, clear with "A" = diurnal  
ambusher; stippled with "A" = nocturnal ambusher;  
vertical-hachures = surface-covering-web; cross-hachures =  
sheet web. Also see Table 3 (axis labelled top left  
diagram). Rare guilds (frequency  $\leq 1\%$ ) not included.  
Plot designations as in Figs. 1 and 2, -7 = 1977, -8 =  
1978. Bars sum to 100%.



attributes of the objects compared, and so the samples with small numbers are allotted deceptively low similarity values. The 1976 sampling period was incomplete and relatively few spiders were collected (Table 2); that is the probable reason for the segregation of some of the 1976 samples (e.g., M3-6, F1-6), and it was considered adequate cause for excluding the 1976 samples from subsequent analyses.

The fir plot (F3), which was considered spruce-like, clusters with typical spruce samples. The fir-like spruce plot (S1) is most similar to one of the fir plots (F2).

When the relative abundances of ground stratum spider species were used as the attributes to compare samples ( $N = 23$ , Fig. 7) a dendrogram similar in most respects to Fig. 6 was produced. There is no level of similarity at which 4 clusters can be discerned; the aspen group included only 4 of the 6 nominal aspen samples.

The relative abundances of species were used as the variables to compare 14 tree samples (Fig. 8). The aspen and conifer samples are probably dissimilar (similarity coefficient = 0.13) because few spiders were collected in the aspen. Among the conifers, samples from the same year but different plot types are more similar than samples from the same tree species during different years. Part of the disparity is due to the data used for analysis. The number of individuals per species differed between 1977 and 1978. However, the species composition of plots remained virtually the same from year to year.

Operationally then, one tree stratum community (hereafter, "tree," community) and 4 ground stratum communities (hereafter, "meadow," "aspen," "fir," and "spruce" communities) are defined. The spiders of ground strata F1 and F2 are considered to be a community of a "fir" habitat, probably

Fig. 6. Cluster analysis of 28 spider assemblages of plots compared by Bray-Curtis Similarity Coefficient (Bray and Curtis, 1957) using relative abundances of spider families from the ground stratum. Plot designations are as in Figs. 1 and 2, -6 = 1976, -7 = 1977, -8 = 1978.

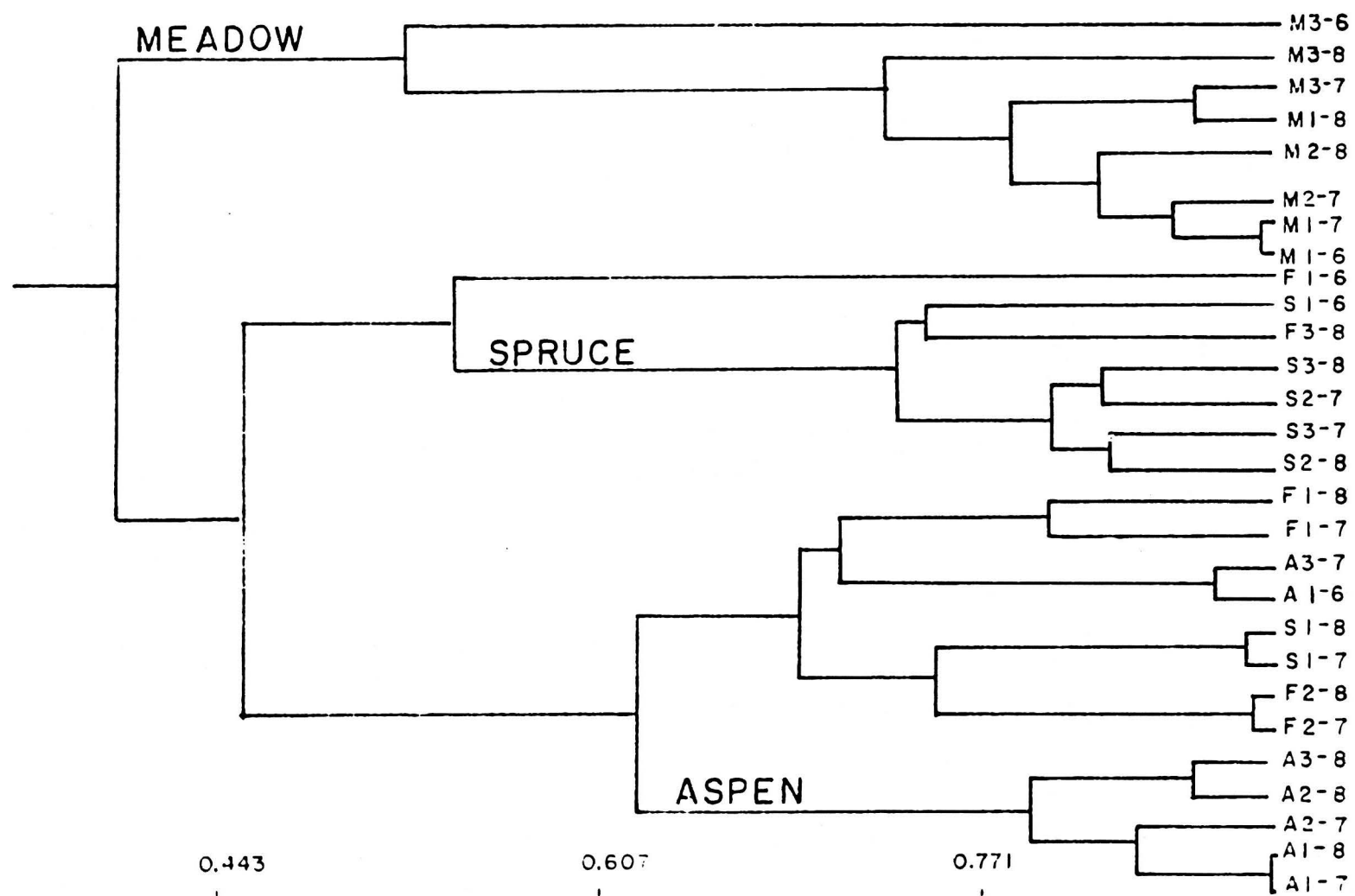




Fig. 7. Cluster analysis of 23 spider assemblages of plots,  
compared by Bray-Curtis Similarity Coefficient, using  
relative abundances of spider species from the ground  
stratum. Plot designations as in Figs. 1 and 2, -7 = 1977,  
-8 = 1978.

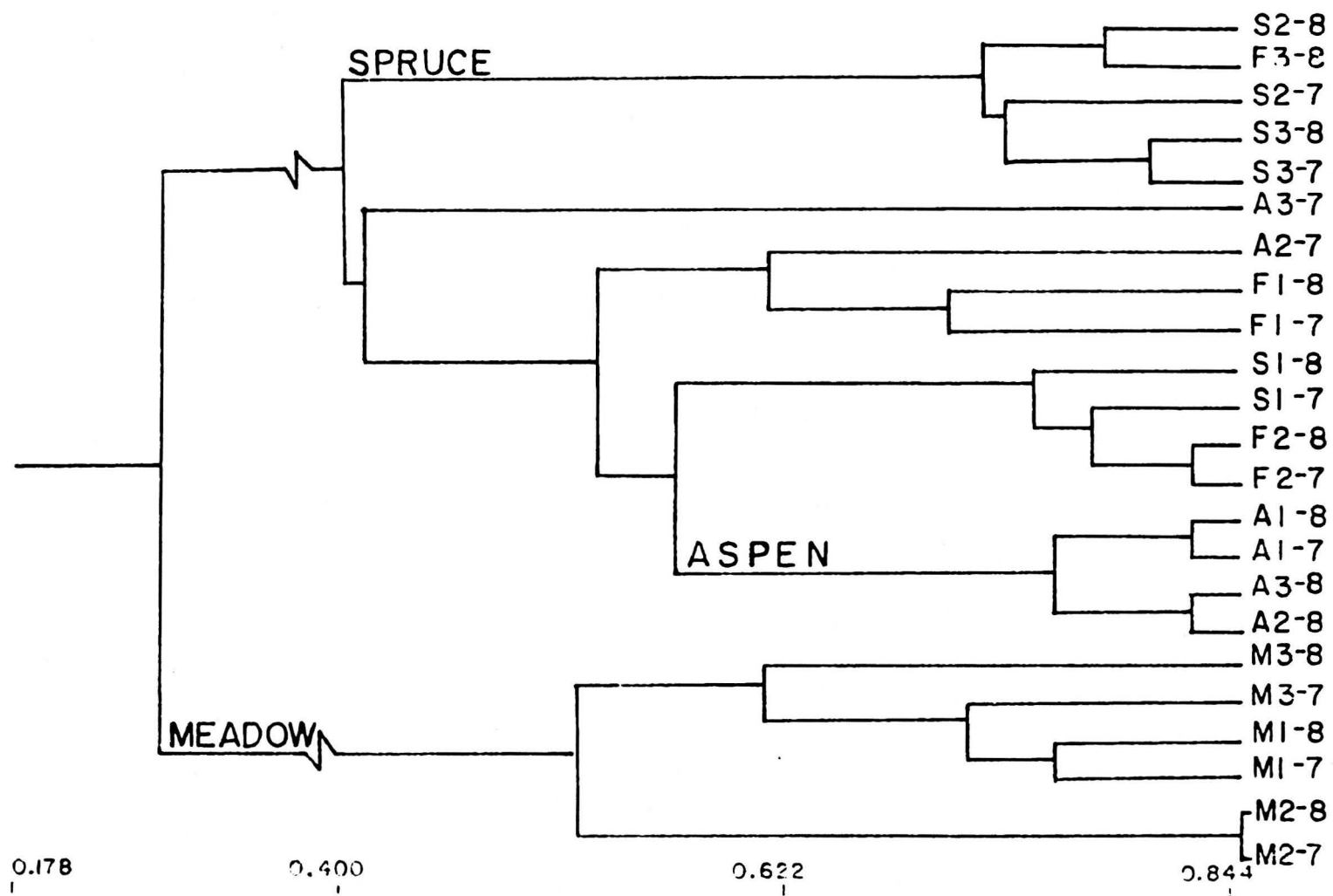
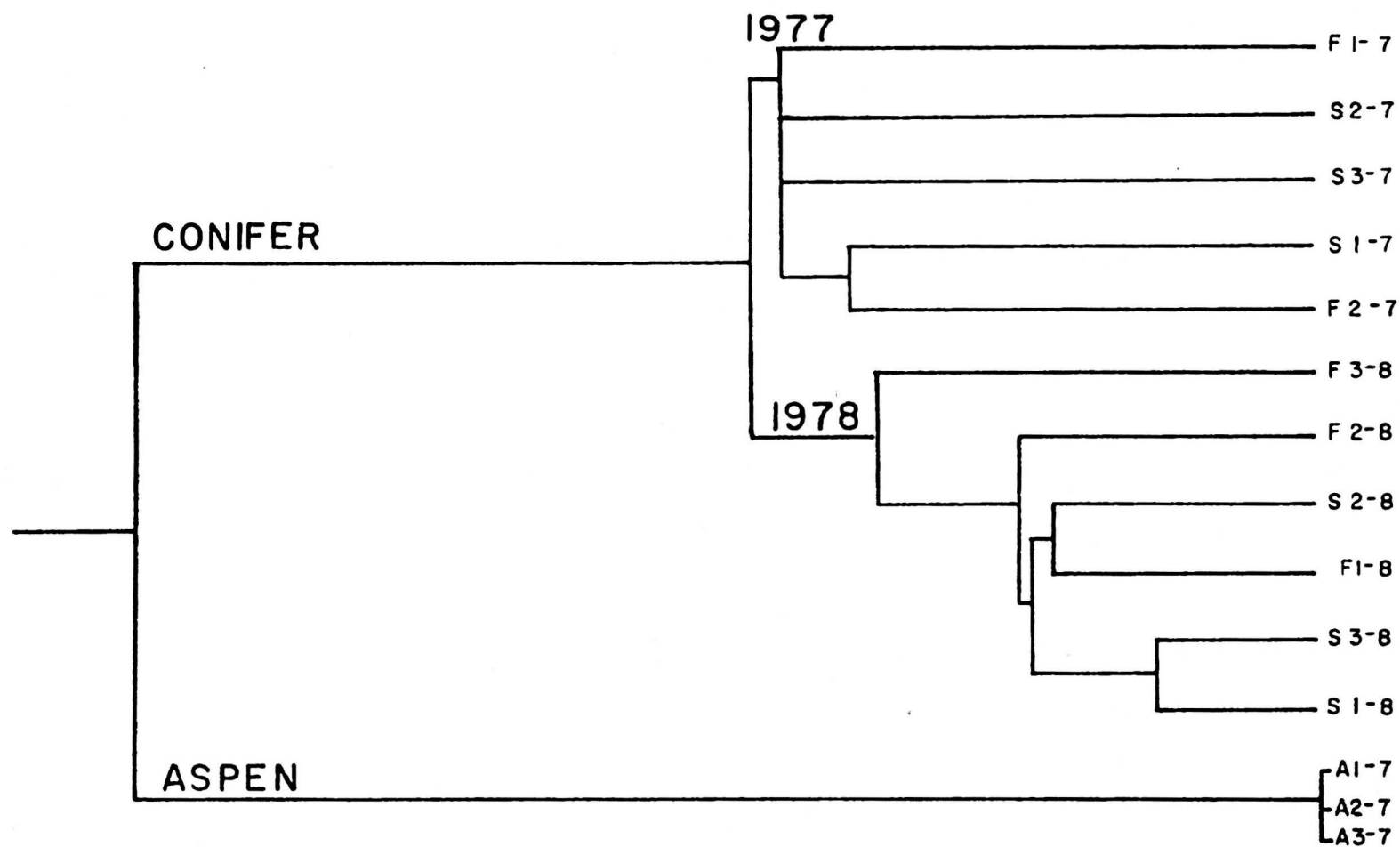


Fig. 8. Cluster analysis of 14 spider assemblages of plots,  
compared by Bray-Curtis Similarity Coefficient using  
relative abundances of spider species from the tree  
stratum. Plot designations are as in Figs. 1 and 2,  
-7 = 1977, -8 = 1978.



0.252

0.544

0.835

having some properties of an ecotone. Spiders of the tree strata of the representative fir and spruce plots together are defined as the single tree stratum community of the sere.

#### Patterns of species abundance

The hypotheses that the relative abundances of spider species in each of the communities are log-series distributions (Fisher et al., 1943) were tested (Fig. 9). The log-series distribution is the best approximation of the species abundance relations for spider communities (Post and Riechert, 1977; Turnbull, 1966). For my data the log-series may be considered the appropriate model for the aspen, fir, and spruce communities. The pattern of species distribution of the tree and meadow communities seems to be geometric (May, 1975; Figs. 10,15). None of the species distributions satisfies Williams' (1964) criterion for a log-normal distribution (i.e., a straight line is obtained when species rank is plotted as accumulated percentage on a probability scale).

Fisher's  $\alpha$  diversity index (an estimate of the number of species represented by a single individual) increases with maturity, although  $\alpha$ -spruce is less than  $\alpha$ -fir (Table 5). The number of incidental species (presumably related to  $\alpha$ ) varies from 13 in the tree community to 28 in the fir, exhibiting the same trend as  $\alpha$ .

#### Characteristic and resident species of the communities

Each of the resident species is considered to be "characteristic" of the community from which the most individuals were collected (Figs. 11-14). The number of accidental species varies from 5 in the fir to 11 in the meadow. The number of resident species varies from 13 in the meadow to 19 in the fir (Table 5, Fig. 15). Because different sampling

Fig. 9. Rank-abundance curves for 5 spider communities.

The null hypothesis tested is that the observed distribution is described by Fisher's log-series model (Fisher et al., 1943).

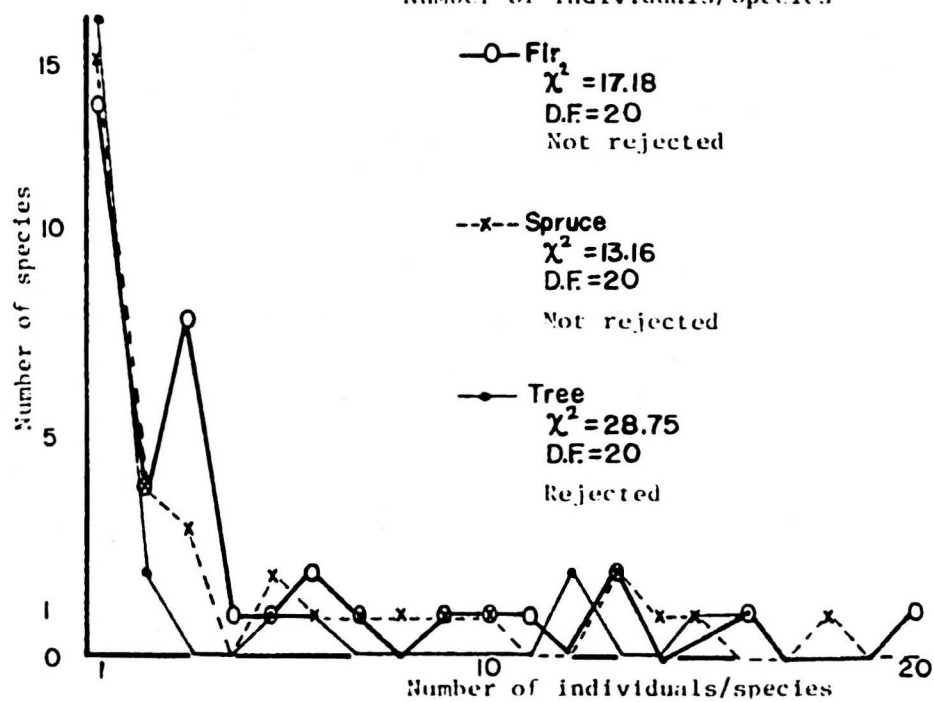
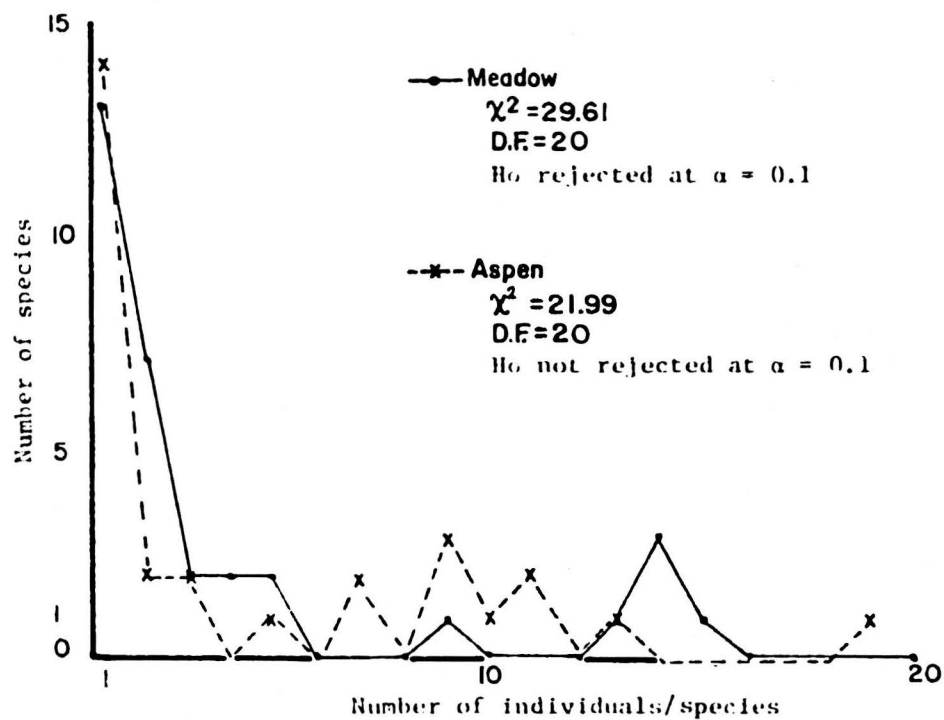


Fig. 10. Dominance-diversity curves for the spider species of 5 communities. Numbers in parentheses are the number of species for which one individual was collected.



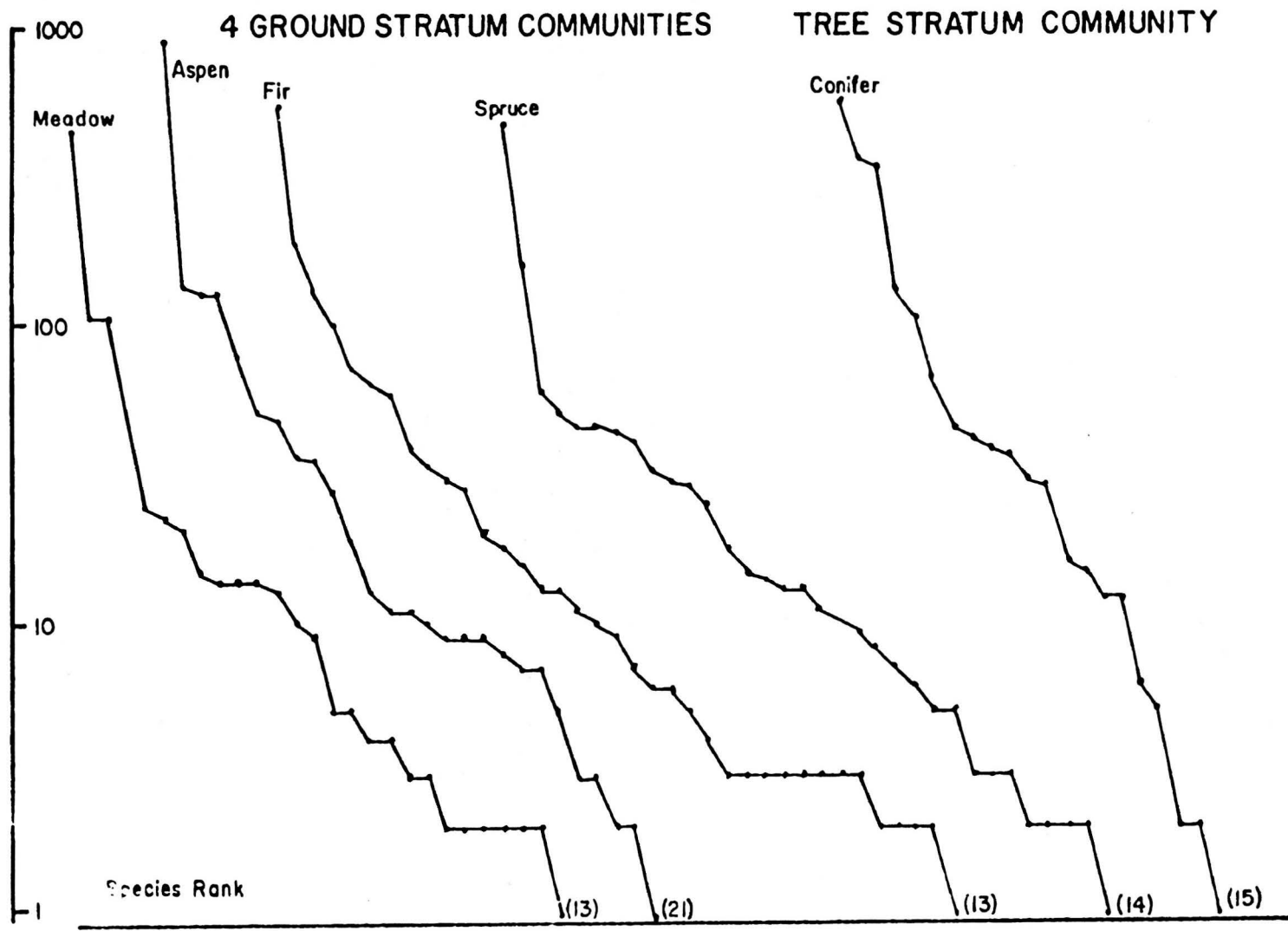


Table 5. Spider community parameters including: total number of species ( $S_T$ ); total number of individuals ( $N_T$ ); Fisher's Diversity Index ( $\alpha$ ); Shannon-Wiener Diversity Index ( $H'$ ); number of characteristic species ( $S_C$ ); number of resident species ( $S_R$ ); frequency of characteristic species ( $S_C/S_R$ ); total number of resident individuals ( $N_R$ ); number of guilds ( $S_G$ ); accidental species ( $S_A$ ); equitability =  $H'/\ln S_R$  ( $J'$ ).

Ground Strata Communities	All Species				Resident Species of Communities								Guilds	
	S <sub>T</sub>	N <sub>T</sub>	α	H'	S <sub>A</sub>	S <sub>C</sub>	S <sub>R</sub>	S <sub>C</sub> /S <sub>R</sub>	N <sub>R</sub>	H'	J'	S <sub>G</sub>	H'	
Meadow	37	946	7.82	2.05	11	9	13	0.69	841	1.55	0.61	5	0.78	
Aspen	46	1785	8.97	2.00	7	8	18	0.44	1714	1.75	0.61	4	0.85	
Fir	49	1507	9.86	2.45	5	5	19	0.26	1422	2.17	0.74	6	1.34	
Spruce	46	1237	9.35	2.46	9	8	16	0.50	1133	2.05	0.74	6	1.42	
Tree Stratum Community														
Conifer	35	2017	6.68	2.11	N/A	(16)	(16)	(1.00)	1889	2.06	0.75	7	1.50	

Fig. 11. Absolute abundances in the ground strata of 4 seral stages of spider species considered to be characteristic of the meadow community. (G1 = Zelotes tuobus, G4 = Drassylus lamprus, C4 = Micaria "B", L3 = Alopecosa kochi, C2 = Scotinella pelvicolens, L5 = Pardosa wyuta, S3 = Talavera minuta, S1 = Pellenes americanus, N1 = Antrodiaetus montanus). Values in parentheses are percentages of resident spiders which are considered accidental because they comprise less than 5 per cent of the individuals collected.

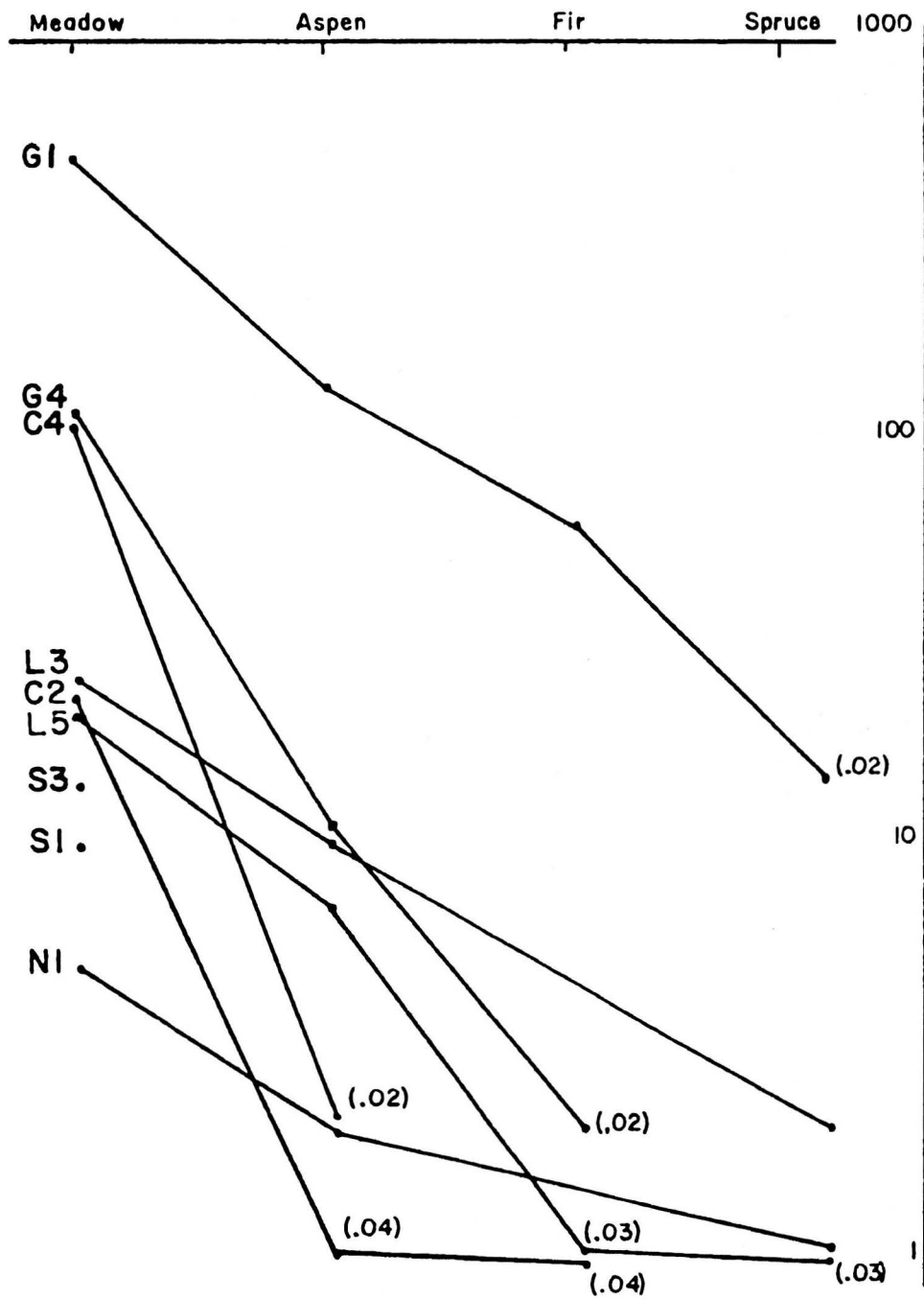


Fig. 12. Absolute abundances in the ground strata of 4 seral stages of spider species considered to be characteristic of the aspen community. (I.2 = Pardosa mackenziana, J3 = Helophora tunagyna, M2 = an unidentified Erigonid, C3 = Micaria "A", K1 = Coreogonai bicornis, G5 = Haplodrassus cunis, M5 = an unidentified Erigonid, K2 = Anacornis proceps).

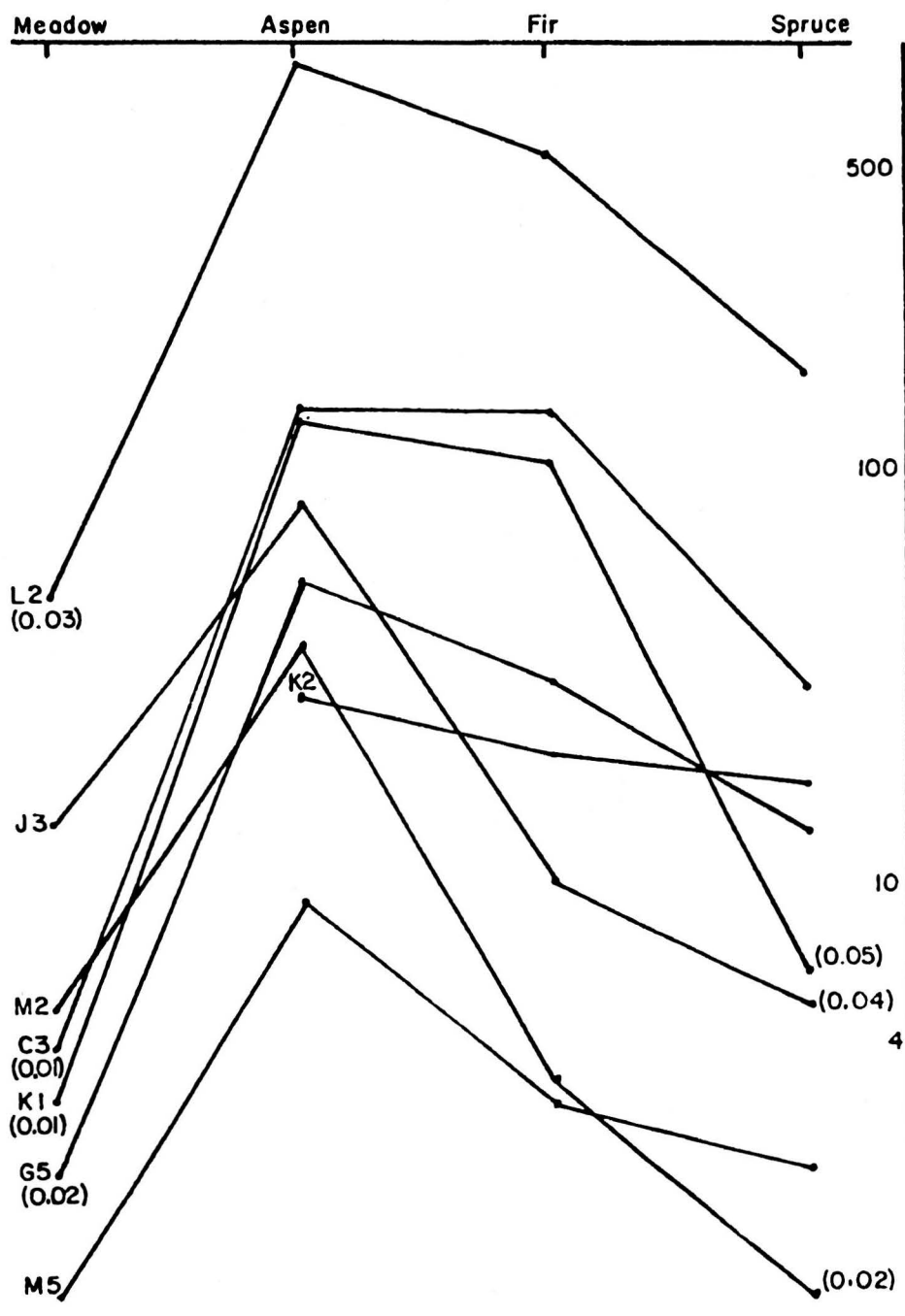


Fig. 13. Absolute abundances in the ground strata of 4 seral stages of spider species considered to be characteristic of the fir ground community. (E1 = Cicurina robusta, L1 = Arctosa alpigena, M6 = an unidentified Erigonid, J6 = Bathyphantes sp., G3 = Gnaphosa muscorum).

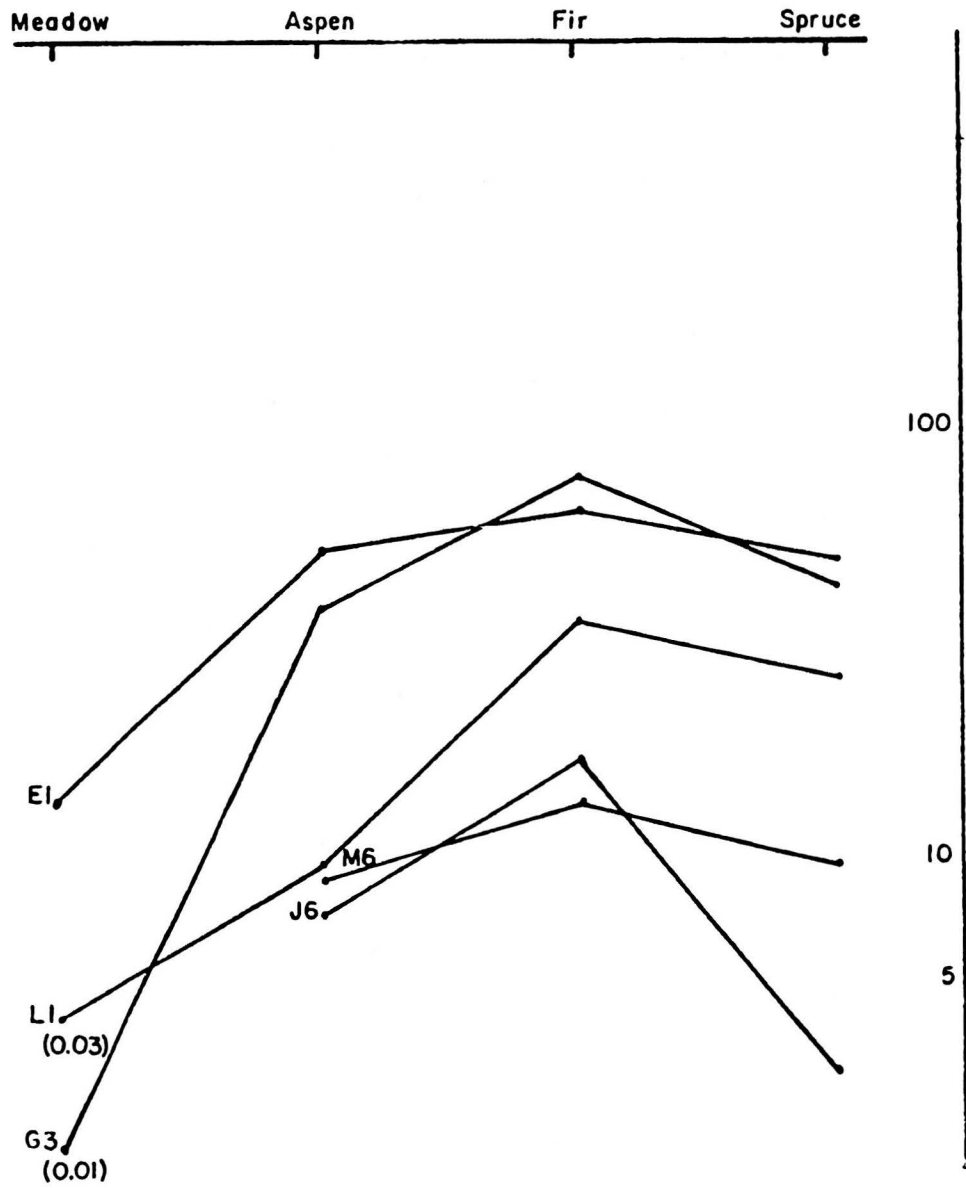




Fig. 14. Absolute abundances in the ground strata of 4 seral stages of spider species considered to be characteristic of the spruce community. (R1 = Callobius norens, M1 = an unidentified Erigonid, M4 = an unidentified Erigonid, G2 = Orodorassus coloradensis, M3 = an unidentified Erigonid, T1 = Steatoda hespera, K3 = Wubana reminescens, M8 = an unidentified Erigonid).

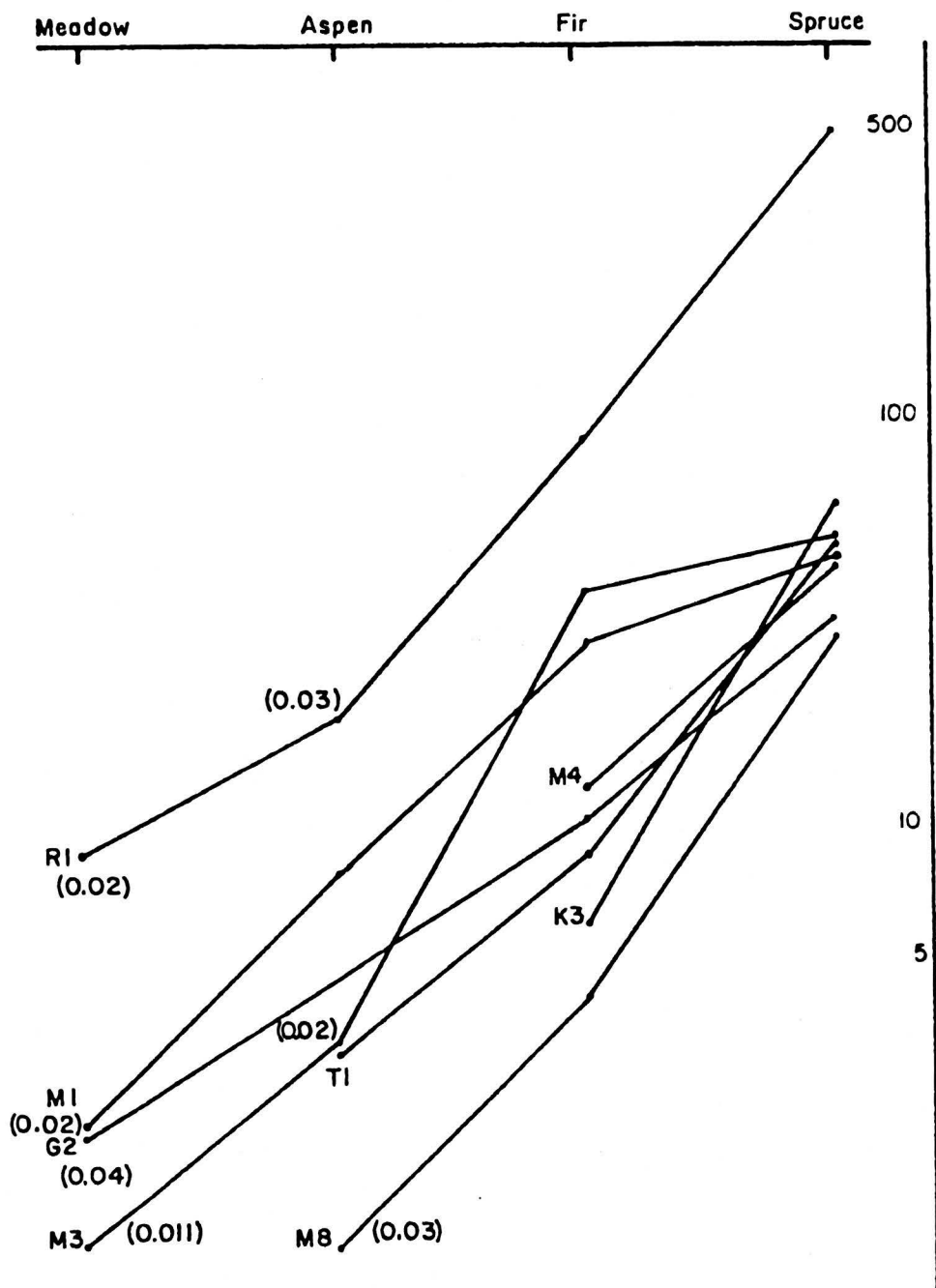
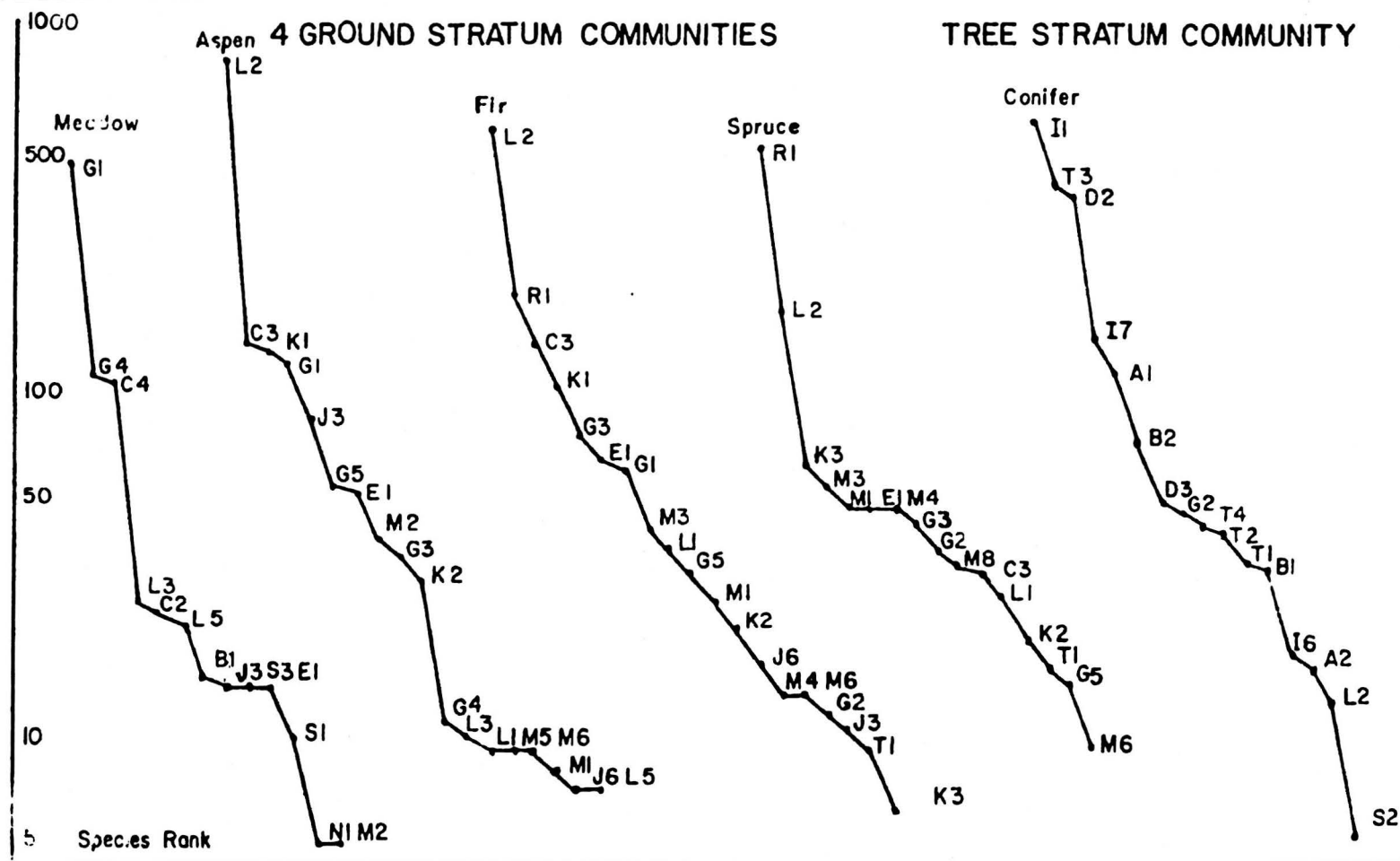


Fig. 15. Dominance-diversity curves for resident spider species  
of 5 communities (for species codes see Table 4).



techniques were employed, the quantitative designations for characteristic and accidental species are not applicable to the tree community spiders, all resident tree spiders are considered characteristic. The number of resident species of a ground community varies inversely with both the number of characteristic species and the number of accidental species (Table 5).

#### Spider distributions and environmental variables

The purpose of canonical correlation analysis (CCA) is to describe the basic relationships between biotic and environmental variables of the same samples (plots). CCA begins with 2 data matrices (Table 6; Figs. 11-14) and "...seeks linear compounds which maximally reveal the joint or common structure of the 2 matrices," (Gauch and Wentworth, 1976). The samples are then ordinated in 2 dimensions (a biotic variable dimension and an environmental variable dimension). The magnitude of the contribution of each variable to the correlation is the loading on the original variable.

The spiders and environmental variables of 12 plots were compared. Of the 5 possible canonical correlations, the first canonical variate was highly significant ( $p < 0.01$ ), for each case (Figs. 16-18), the remaining 4 variates were not significant ( $p > 0.05$ ).

The 9 environmental variables (Table 6) segregate into 3 fairly consistent groups. The meadow factor (M.F.) consists of one environmental variable (bare dirt); the aspen factor (A.F. consists of 2 variables (grasses and forbs, low foliage index); and the spruce factor (S.F.) consists of 5 associated variables (litter depth, tree basal area, canopy cover, dead leaves and needles, logs). The high-foliage index was not correlated to any biotic variable and so was non-informative (Table 6).

Fig. 16. Canonical correlation of environmental variables  
(Table 6) to spider species with different foraging  
strategies (loadings in parentheses); M.F. = meadow  
factor, A.F. = aspen factor, S.F. = spruce factor.

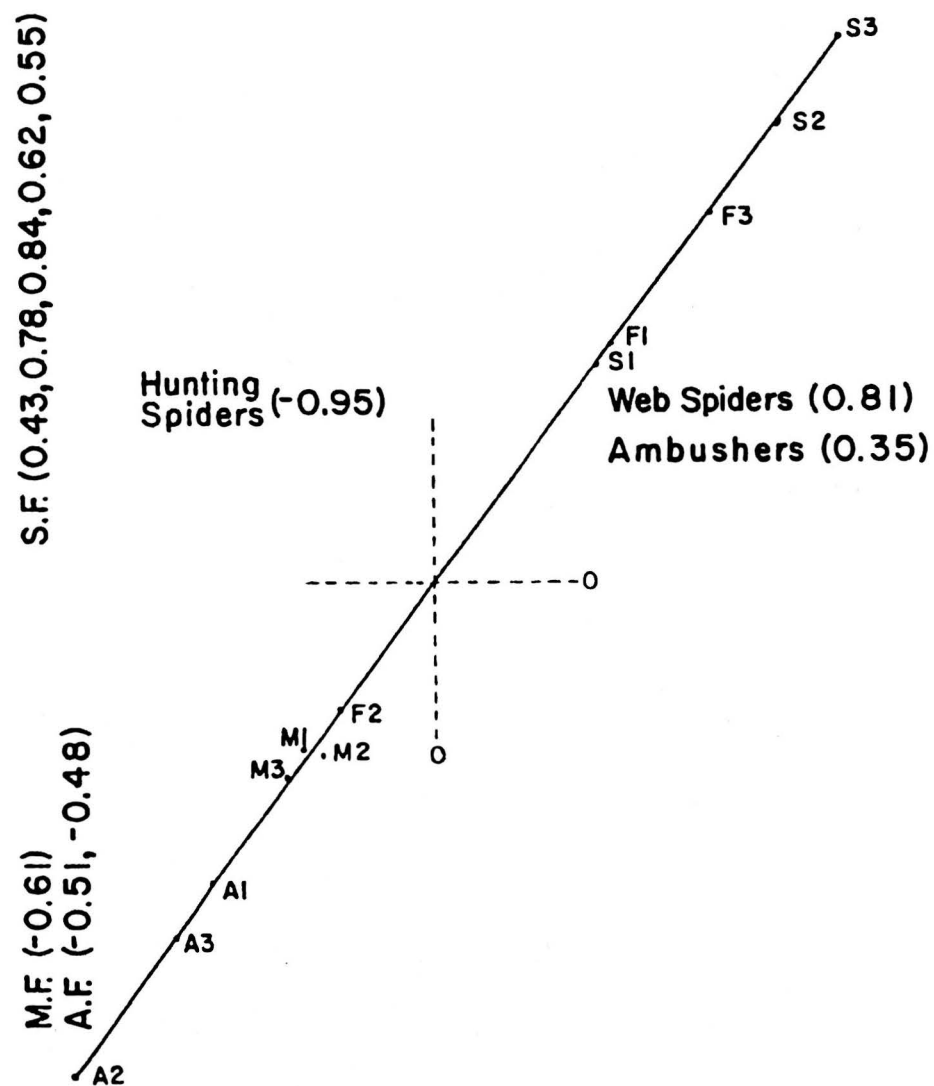


Fig. 17. Left, canonical correlation of environmental variables with characteristic species of the meadow community. Right, canonical correlation of environmental variables with characteristic species of the aspen community. (Environmental variables of S.F. indicated by asterisk, Table 6). M.F. = meadow factor, A.F. = aspen factor, S.F. = spruce factor, for other abbreviations see Table 6. (C2 = Scotinella pelviocolens, C4 = Micaria "B", G1 = Zelotes tuobus, G4 = Drassylus lamprus, L3 = Alopecosa kochi, L5 = Pardosa wyuta, C3 = Micaria "A", J3 = Helophora tunagyna, K1 = Coreogonol bicornis, L2 = Pardosa mackenziana, M2 = an unidentified Erigonid).



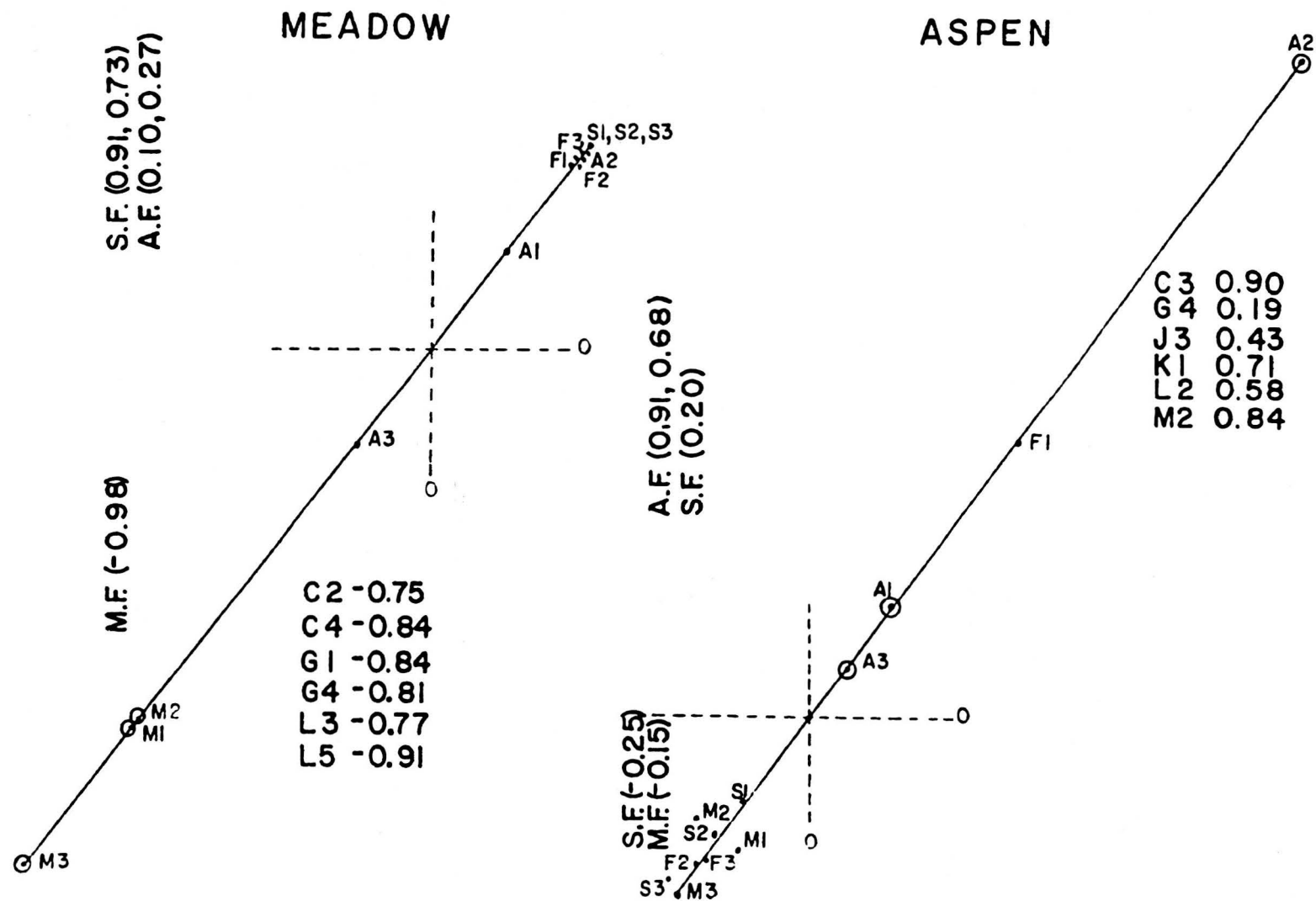
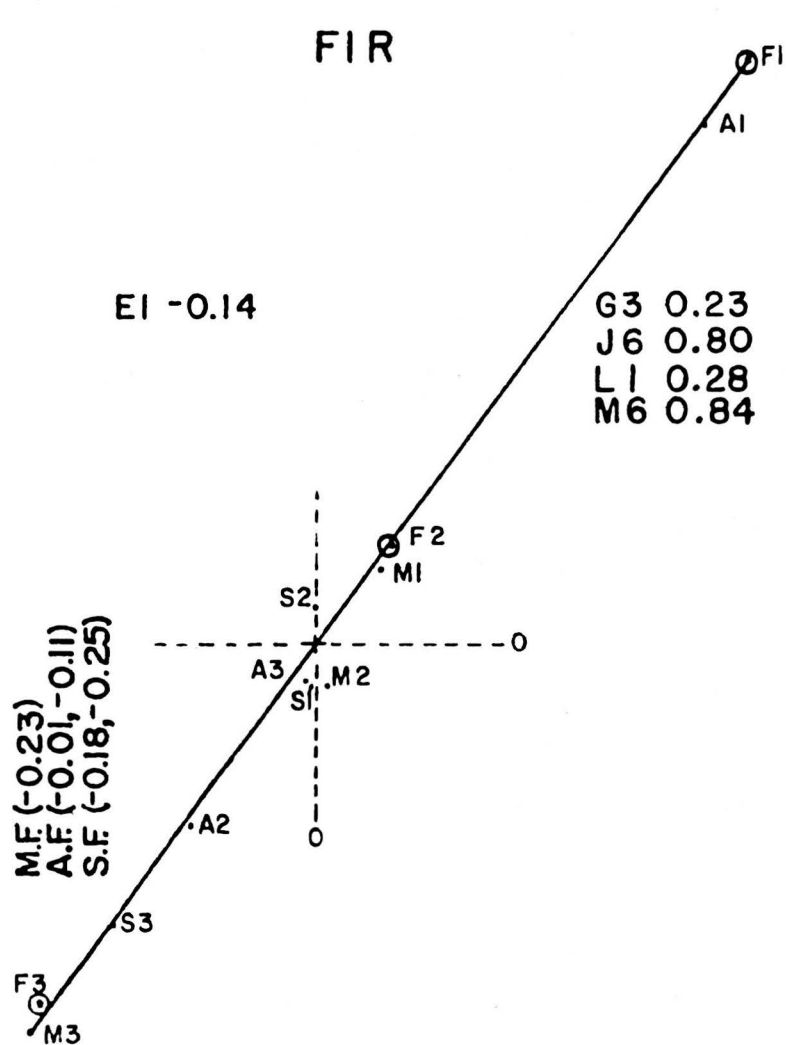


Fig. 18. Left, canonical correlation of environmental variables with characteristic species of the fir community. Right, canonical correlation of environmental variables with characteristic species of the spruce community. (Environmental variables of S.F. community indicated by asterisk, Table 6). M.F. = meadow factor, A.F. = aspen factor, S.F. = spruce factor, for other abbreviations see Table 6. (G3 = Gnaphosa muscorum, J6 = Bathypantes sp., L1 = Arctosa alpicena, M6 = an unidentified Erigonid, G2 = Orodorassus coloradensis, K3 = Wubana reminescens, M1 = an unidentified Erigonid, M3 = an unidentified Erigonid, M4 = an unidentified Erigonid, R1 = Callobius nomeus).

# FIR



# SPRUCE

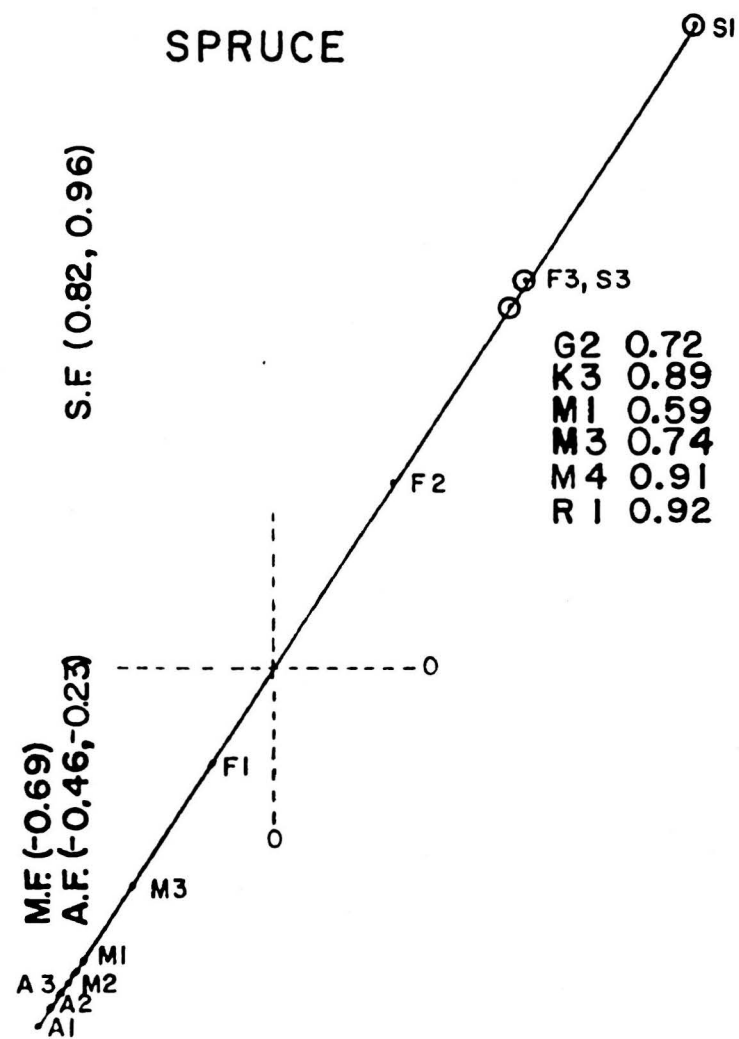


Table 6. Values for 9 environmental variables in 12 plots of a spruce-fir sere. See text for "index" units and methods of derivation. Asterisks indicate spruce factor variables used in Figs. 17-18.

Plots	FACTORS								
	Meadow	Aspen		Spruce					High Foliage Index
	Bare Dirt (%)	Grasses & Forbs (%)	Low Foliage Index	Canopy Cover (%)	Litter * Depth (cm) ( $\bar{x}$ (S.D.))	Dead Leaves (%)	Logs (%)	Tree Basal* Area (%)	
M1	43.0	40.2	69.0			6.8	0		43.0
M2	42.6	52.2	94.5			7.9	0		50.5
M3	56.2	39.3	103.0			4.5	0		87.0
A1	11.7	31.4	87.0	76.4	0.72(0.48)	44.1	12.5	0.19	86.0
A2	14.5	30.0	96.5	65.4	0.86(0.26)	42.8	12.2	0.12	133.5
A3	30.1	22.0	84.5	81.8	0.16(0.15)	38.0	9.9	0.22	194.5
F1	1.7	10.0	44.5	64.9	5.64(2.07)	56.9	31.7	0.18	120.5
F2	6.3	1.1	48.5	63.5	1.54(1.55)	62.2	30.4	0.23	193.5
F3	0	28.1	42.0	85.8	4.08(0.91)	54.6	17.3	0.59	175.0
S1	0	3.2	23.5	75.8	6.5(3.3)	49.7	46.9	0.37	110.5

Table 6. Continued

FACTORS									
Plots	Meadow	Aspen		Spruce				None	
	Bare Dirt (%)	Grasses & Forbs (%)	Low Foliage Index	Canopy Cover (%)	Litter Depth (cm) ( $\bar{x}$ (S.D.))	Dead Leaves (%)	Logs (%)	Tree Basal Area (%)	High Foliage Index
S2	0	0	7.0	83.3	5.66(1.46)	83.1	16.9	0.45	57.0
S3	0	2.1	30.0	90.7	4.80(1.96)	67.4	30.5	0.55	82.0

Of the 3 ecological spider strategies (Table 3), hunting spiders are related positively to the M.F. and the A.F. variables and web-spiders to the S.F. variables. The correlation of ambushers to the S.F., though positive, is not significant (loading  $< 0.50$ ; Fig. 16). The characteristic spiders of the meadow, aspen, and spruce communities are positively correlated to the meadow, aspen, and spruce factors respectively (Figs. 17, 18). The inverse correlations of the S.F. to the meadow spiders and the M.F. to the spruce spiders are significant (loading  $> 0.50$ ). All of the non-aspen spiders except Cicurina robusta, a characteristic fir spider, are correlated inversely to the A.F., but none of the loadings is significant.

Four of the 5 characteristic fir spiders (Arctosa alpigena, Bathypantes sp, Cicurina robusta, an unidentified erigonid, M6) are inversely correlated (2 significantly, Bathypantes sp, and an unidentified erigonid, M6) to all 3 environmental factors (Fig. 19). I conclude that the distribution of fir spiders is not significantly correlated to the environmental variables measured.

#### Resource use by the resident species of the communities

In the time dimension spider species are distributed along seasonal and daily axes (Figs. 19-23); in space they occupy different habitats (Figs. 16-18) and microhabitats (Figs. 24-25; Tables 7-8). The size of prey taken (Enders, 1976) and the foraging rate of active hunters (Fig. 25, Table 9) are both related to body size, the former positively, and the latter negatively.

#### Community parameters

There are 2 phenological patterns of spider biomass. In the ground

Fig. 19. Guild affiliation and variation in daily and seasonal activity of resident spider species of the meadow ground stratum community. Center of circle = mean date (males); horizontal line = mean date  $\pm$  1 S.D.; and size (radius of circle = average B.L. of males). Daily activity is not represented for web-spiders. Alopecosa kochi (L3) is probably represented by 2 populations, individuals were diurnal ambushers in the early spring and nocturnal ambushers in the fall.

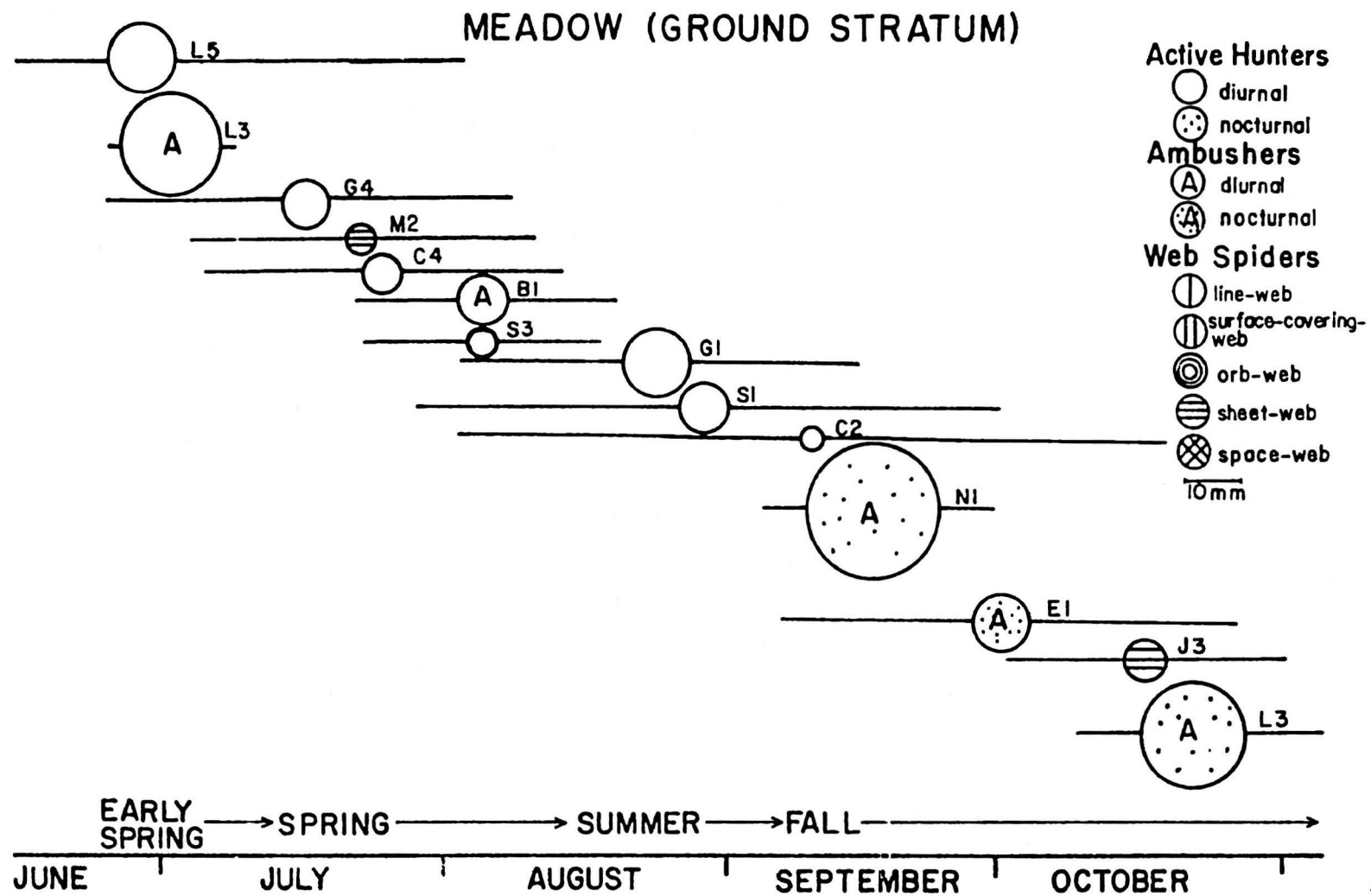




Fig. 20. Guild affiliation and variation in daily and seasonal activity of resident spider species of the aspen ground stratum community. Center of circle = mean date (males); horizontal line = mean date  $\pm$  1 S.D.; and size (radius of circle = average B.L. of males).

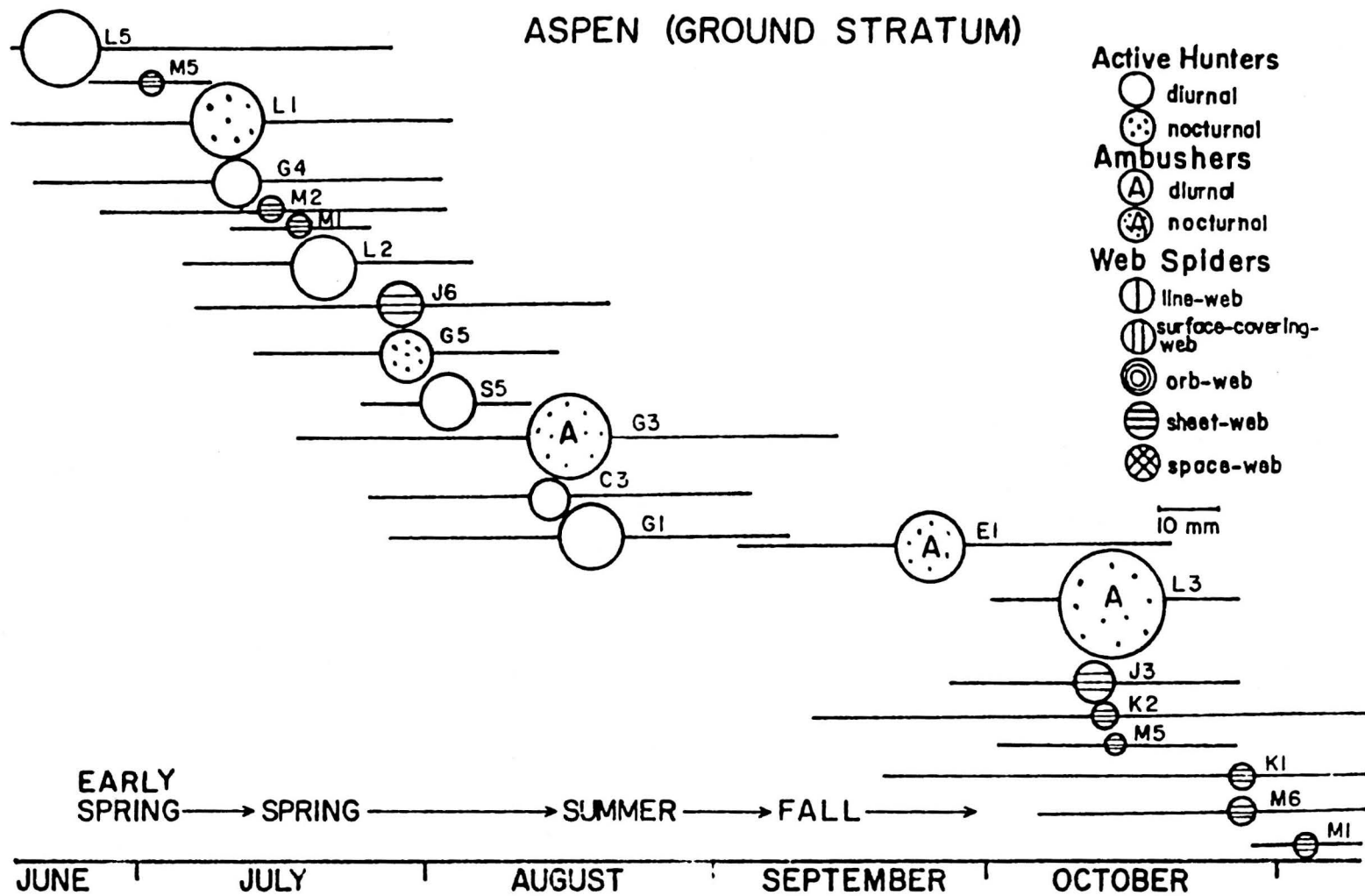


Fig. 21. Guild affiliation and variation in daily and seasonal activity of resident spider species of the fir ground stratum community. Center of circle = mean date (males); horizontal line = mean date  $\pm$  1 S.D.; and size (radius of circle = average B.L. of males.

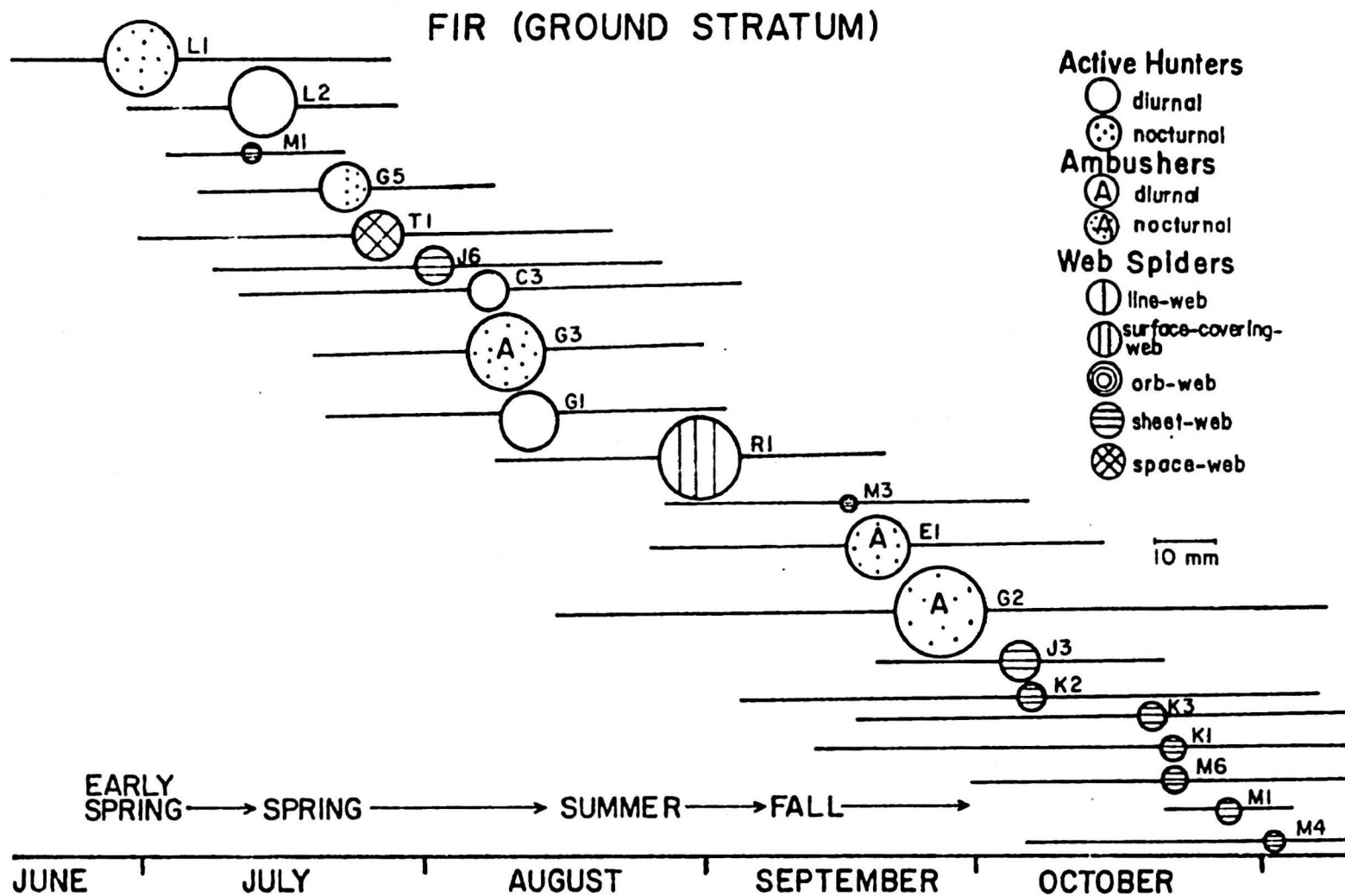


Fig. 22. Guild affiliation and variation in daily and seasonal activity of resident spider species of the spruce ground stratum community. Center of circle = mean date (males), horizontal line = mean date  $\pm$  1 S.D.: and size (radius of circle = average B.L. of males).

# SPRUCE (GROUND STRATUM)

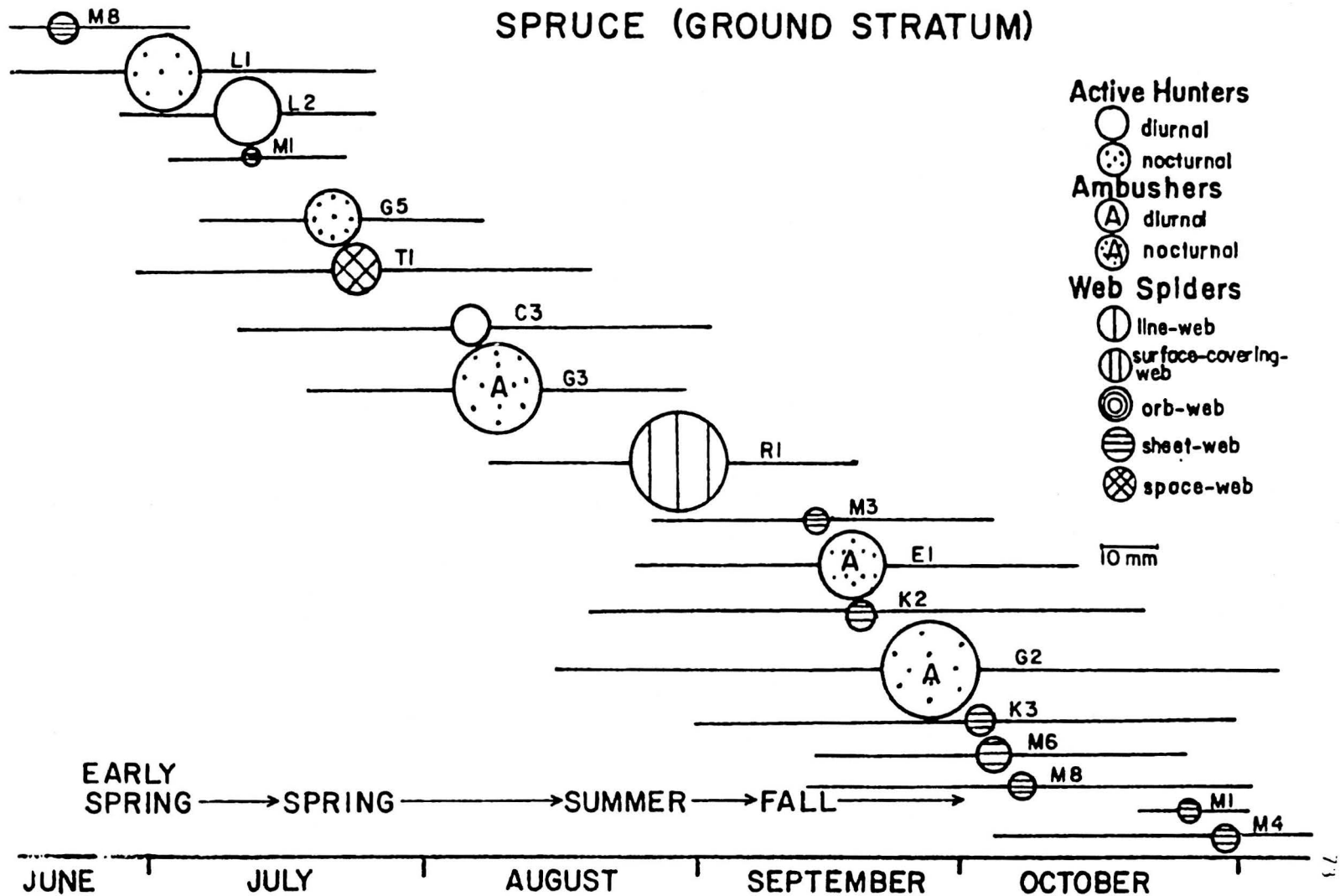


Fig. 23. Guild affiliation and variation in daily and seasonal activity of resident spider species of the conifer tree stratum community. Center of circle = mean date (males); horizontal line = mean date  $\pm$  1 S.D.; and size (radius of circle = average B.L. of males).

# CONIFER (TREE STRATUM)

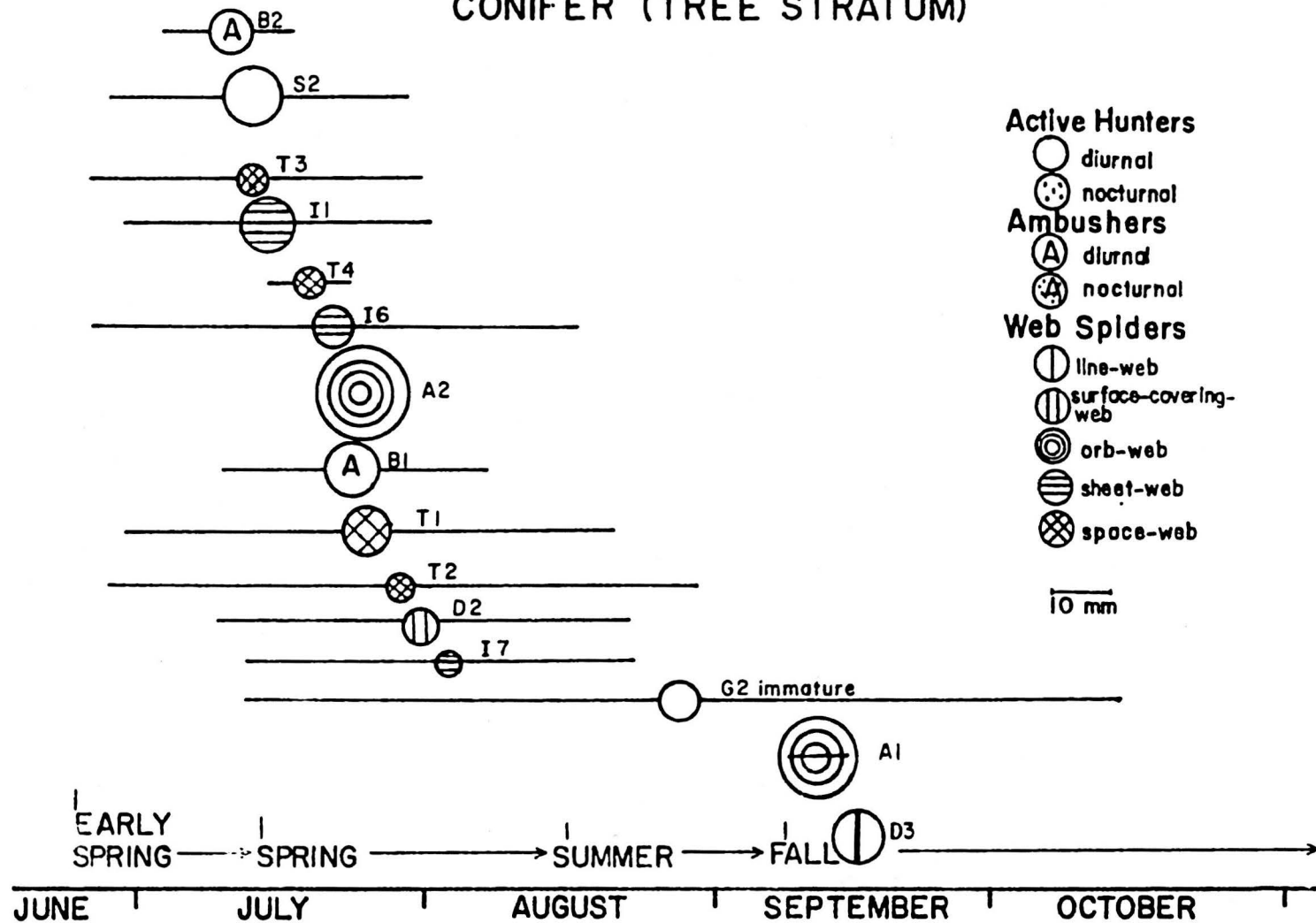




Fig. 24. Horizontal and vertical location of spider webs in relation to tree trunk and canopy. Scale refers to size of web = diameter of circle, for species code see Table 4. See Appendix II for details of web measurement methodology.

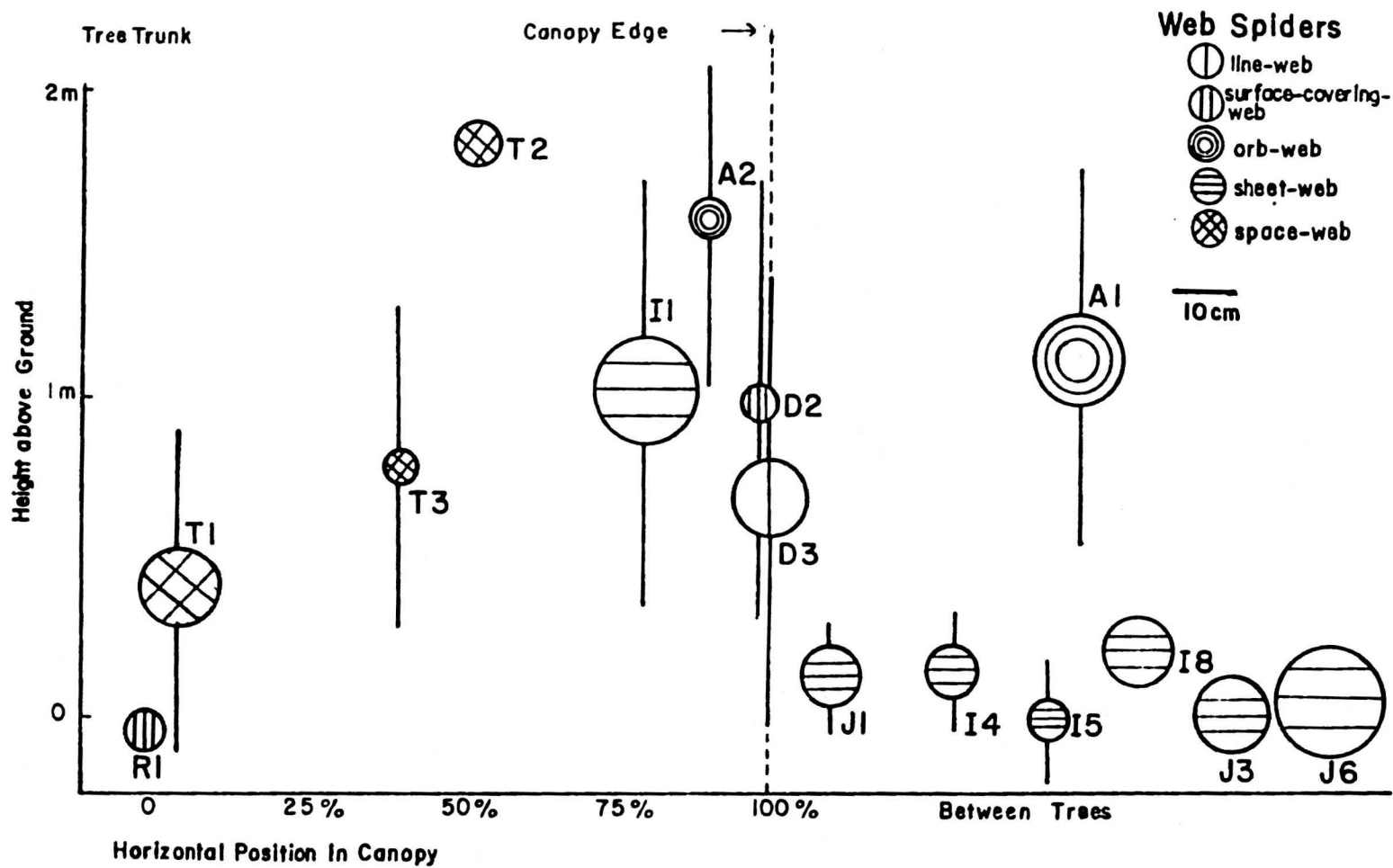
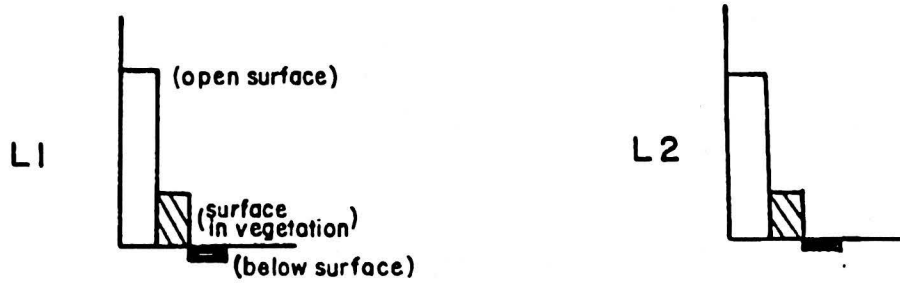
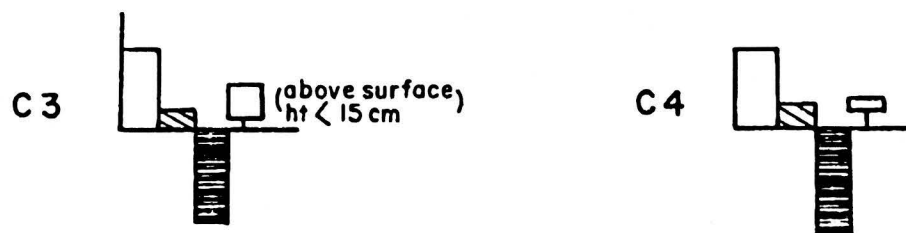


Fig. 25. Microhabitat occupancy time by 8 active hunting spider species. Bars sum to 100%. (L1 = Arctosa alpigena, L2 = Pardosa mackenziana, C3 = Micaria "A", C4 = Micaria "B", G1 = Zelotes tuobus, S1 = Pellenes americanus, S5 = Pellenes laggani, S2 = Metaphidippus aeneolus).

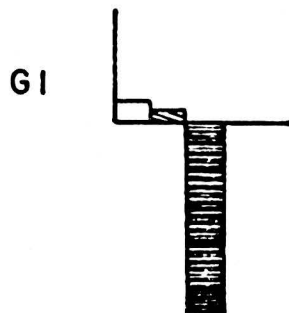
## F. LYCOSIDAE



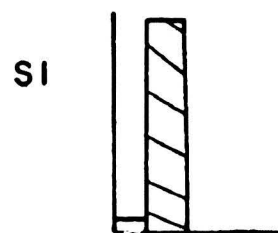
## F. CLUBIONIDAE



## F. GNAPHOSIDAE



## F. SALTICIDAE



## F. SALTICIDAE



Fig. 26. Linear regression for rate of movement against body size for 14 hunting spider species.

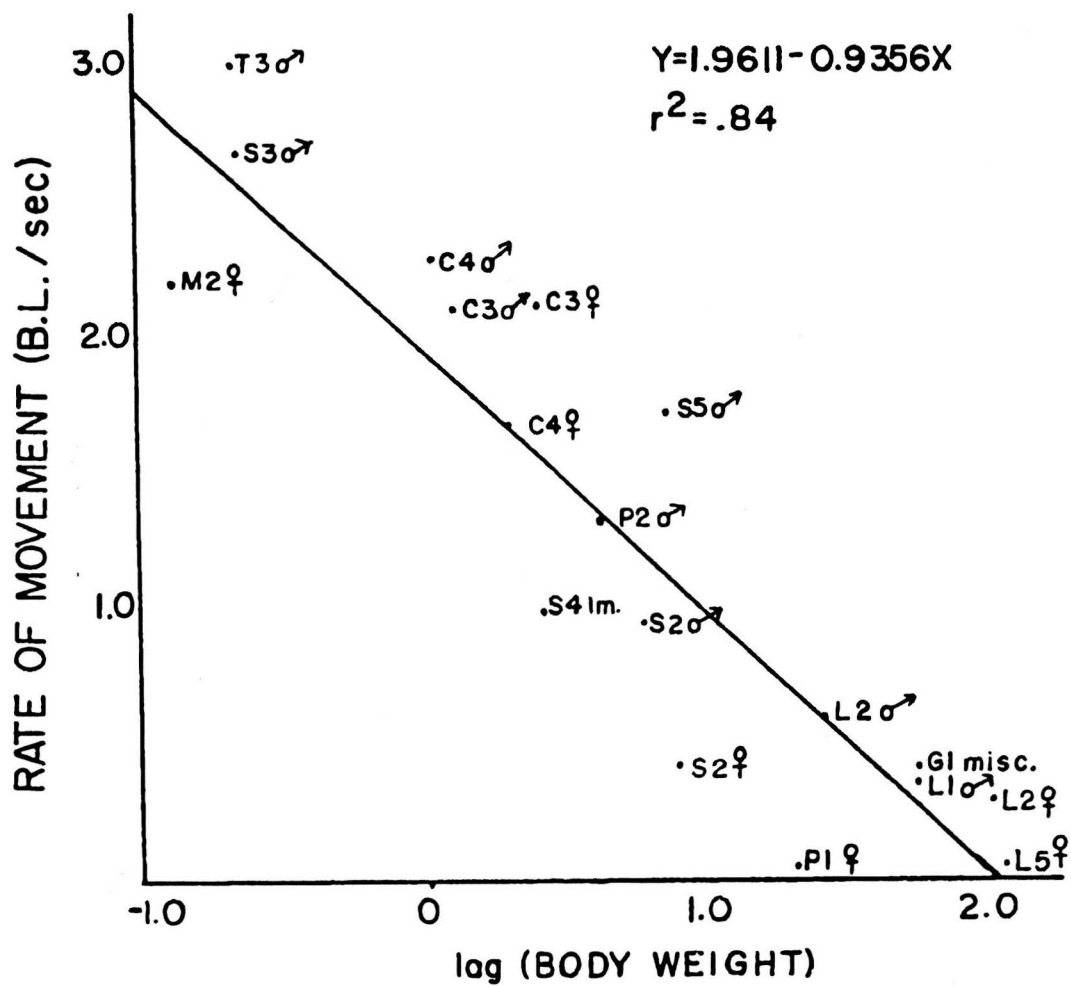


Table 7. Web location and web size for 15 web-spider species. Index of centrality refers to horizontal position in canopy between 0 on tree trunk and 100% on canopy edge. N/A = not applicable.

Species	Ht: $\bar{X}(n, S.D.)$	Size: $\bar{X}(n, S.D.)$ (cm)	Index of Peripherality
<b>Amaurobiidae</b>			
R1	-2.3(3, 2.5)	6.5(4, 2.4)	0%
<b>Araneidae</b>			
A1	116.6(14, 56.7)	14.4(14, 21.6)	N/A
A2	161.0(4, 49.8)	5.5(4, 0.58)	N/A
<b>Dictynidae</b>			
D2	102.1(12, 69.2)	5.1(9, 2.9)	100%
D3	73.3(14, 7.18)	12.4(13, 3.6)	100%
<b>Linyphiidae</b>			
I1	105.0(51, 67.2)	17.2(44, 9.6)	81%
I4	15.3(16, 18.7)	7.8(15, 2.7)	13%
I5	0.2(2, 21.2)	6.5(2, 2.1)	N/A
I8	25.0(3, 8.7)	11.3(3, 1.2)	N/A
J1	15.3(7, 16.5)	10.1(7, 3.0)	0%
J3	2.0(1, 0.0)	11.6(3, 1.5)	N/A
J6	9.0(2, 1.4)	9.0(2, 1.4)	N/A
<b>Theridiidae</b>			
T1	40.9(17, 51.6)	12.2(13, 7.6)	4%
T2	182.0(2, 2.8)	7.0(3, 3.0)	55%
T3	82.1(12, 53.3)	5.7(11, 5.1)	42%

Table 8. Microhabitat occupancy time (secs) of 18 hunting spider species.

Family Species	Open Surface	Ground Surface with Plant Bases	Below Surface	Above Surface ht < 15 cm	Above Surface ht > 15 cm	Total (n, sec)
<b>F. Clubionidae</b>						
C3 M	240	180	630	75		(3, 1125)
C3 F	755	60	570	235		(4, 1620)
C4 M	60	105	30			(1, 195)
C4 F	405	150	975	90		(4, 1620)
C4 im	315	15	30	15		(1, 375)
<b>F. Erigonidae</b>						
M2 F	135			155		(1, 290)
<b>F. Gnaphosidae</b>						
G1	210	90	1800			(6, 2100)
<b>F. Lycosidae</b>						
L1 M	285	60	30			(1, 375)
L2 M	885	30	75			(4, 990)
L2 F	405	30	120			(2, 555)
L2 im	2358	1185	120			(10, 3663)



Table 8. Continued.

Family	Open Surface	Ground Surface with Plant Bases	Below Surface	Above Surface ht < 15 cm	Above Surface ht > 15 cm	Total (n, sec)
F. Lycosidae (continued)						
L3 M	675		75			(2, 750)
L3 F	1020					(1, 1020)
L5 F	480	270				(2, 750)
F. Philodromidae						
P1 F	120			2460		(2, 2580)
P2 M				405	75	(1, 480)
F. Salticidae						
S1 F	360	15				(1, 375)
S2 M				945		(3, 945)
S2 F				495		(1, 495)
S3 M	465	750	285			(4, 1500)
S4 fm	375					(1, 375)
S5 M	1200	315	30	240		(4, 1785)

Table 8. Continued.

Family	Open Surface	Ground Surface with Plant Bases	Below Surface	Above Surface ht < 15 cm	Above Surface ht > 15 cm	Total (n, sec)
F. Salticidae (continued)						
S5 im	990	375	30			(2, 1395)
S6 F					375	(1, 375)
F. Theridiidae						
T2 M					181	(1, 181)
T3 M					750	(2, 750)

Table 9. Values for size and rate of movement parameters for 16 spider species.

Taxon	Sex (n)	B.L. (mm)	No. 15 sec Intervals	mm/sec	B.L./sec	ln(body weight) (mg)
<b>Clubionidae</b>						
C3	M(3)	3.41	75	7.1	2.082	0.104
C3	F(4)	3.84	108	7.9	2.06	0.38
C4	M(1)	3.31	13	7.5	2.28	0.04
C4	F(4)	3.71	108	6.2	1.67	0.30
<b>Erigonidae</b>						
M2	F(1)	1.9	19	4.2	2.21	-0.88
<b>Gnaphosidae</b>						
G1	Misc(6)	6.0	140	2.6	0.433	1.77
<b>Lycosidae</b>						
L1	M(1)	5.99	25	2.2	0.37	1.77
L2	M(4)	5.49	66	3.5	0.64	1.44
L2	F(2)	6.43	37	2.2	0.34	2.05
L3	M(2)	9.31	45	0.7	0.075	3.9
L3	F(1)	10.36	68	0	0	4.58
L5	F(2)	6.47	50	2.6	0.04	2.08
<b>Philodromidae</b>						
B1	F(2)	5.50	165	0.3	0.06	1.45
B2	M(1)	4.25	32	5.6	1.32	0.64
<b>Salticidae</b>						
S1	F(1)		25			
S2	M(3)	4.48	63	4.2	0.9375	0.79
S2	F(1)	4.67	33	1.9	0.42	0.92

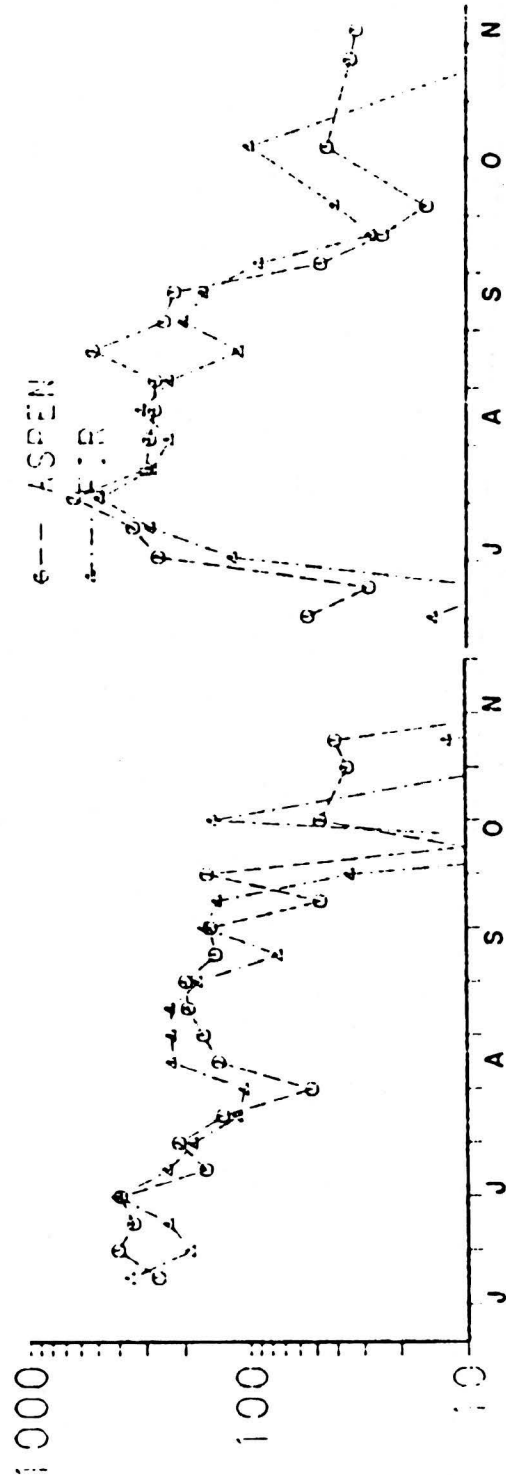
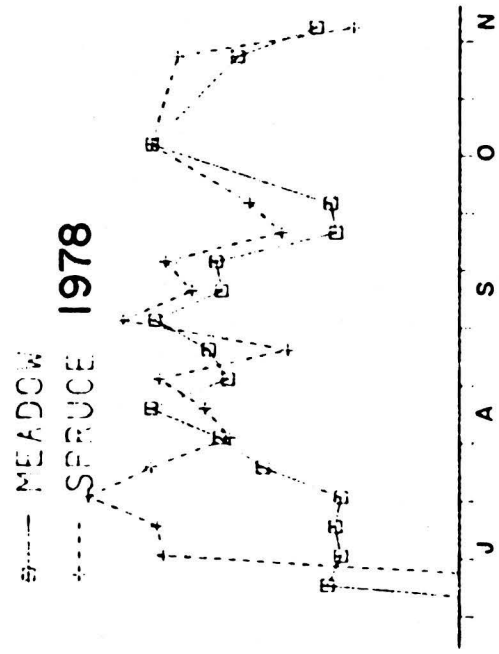
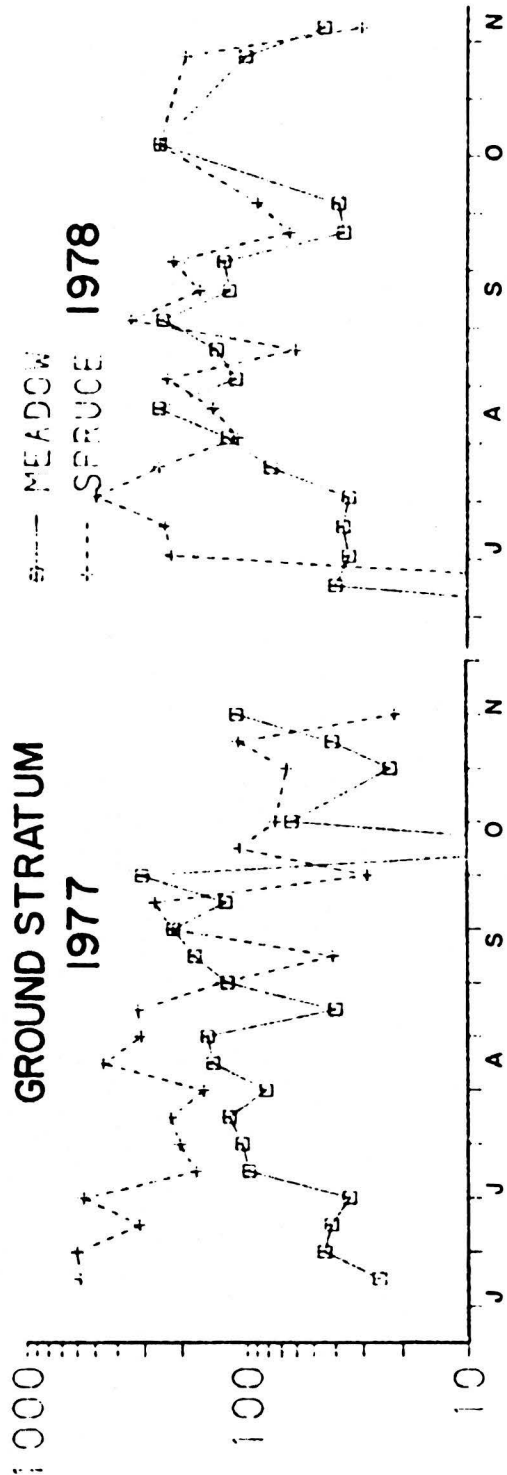
Table 9. Continued

Taxon	Sex (n)	B.L. (mm)	No. 15 sec Intervals	mm/sec	B.L./sec	ln(body weight) (mg)
Salticidae (continued)						
S3	M(4)	2.2	100	0.8	2.7	-0.67
S4	Im(1)	3.9	33	3.9	1.00	0.42
S5	M(4)	4.6	119	7.9	1.72	0.87
Theridiidae						
T3	M(2)	2.16	50	6.5	3.01	-0.66

stratum communities, of the forest the maximum biomass occurs in the spring, there is a secondary mid-summer peak and a fall peak. The pattern is similar to that observed in other spider communities (MacMahon and Trigg, 1972; Peck, 1966). In the meadow and tree strata there is no spring peak and maximum biomass occurs in the fall (Figs. 27-28).

In the ground stratum communities from meadow to spruce stages, total biomass of spiders average size, proportion of web-spiders, semi-annual, biennial, and nocturnal spiders increase monotonically (Figs. 29-31). Two measures of species diversity, Fisher's  $\alpha$  Index and the Shannon-Wiener Information Theoretic Index, follow the same trend (Table 5, Fig. 31).

Fig. 27. Changes in spider biomass over the 1977 and 1978 field seasons in 4 ground stratum communities.



Biomass (mg/plot)

Fig. 28. Changes in spider biomass over the 1977 and 1978 field seasons in fir and spruce tree strata spiders.



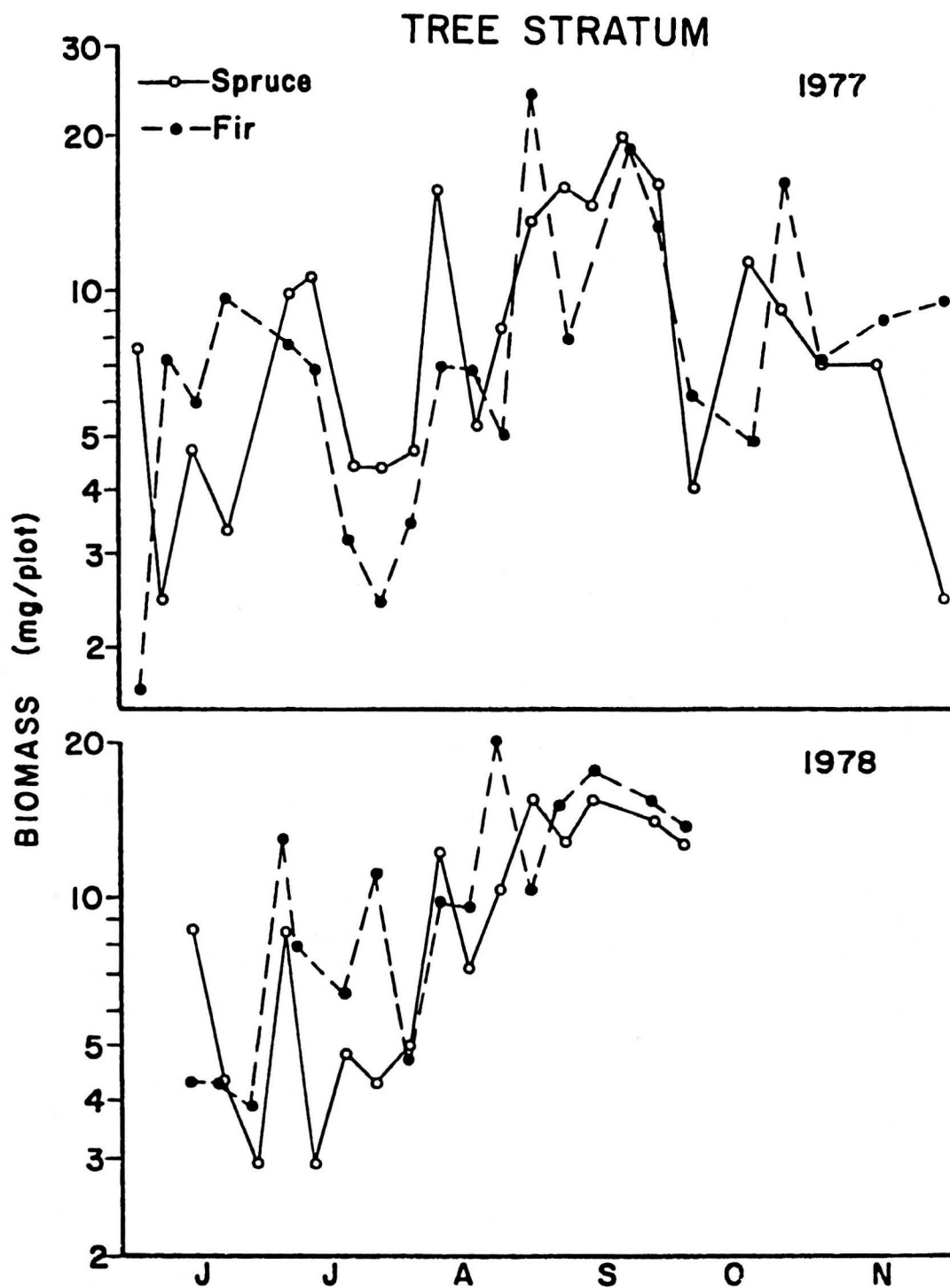


Fig 29. Top, total biomass (mg/yr) in 4 ground stratum communities of a spruce-fir sere for the years 1977 and 1978. Bottom, average body length (B.L.) of adults of 4 ground stratum communities of a spruce-fir sere, 1977 plus 1978 data pooled.

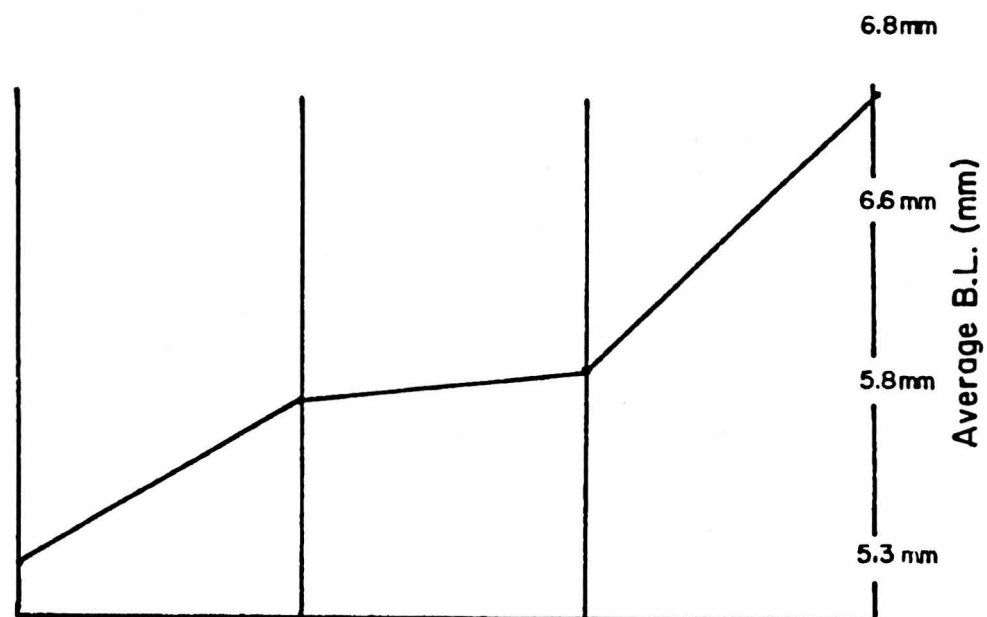
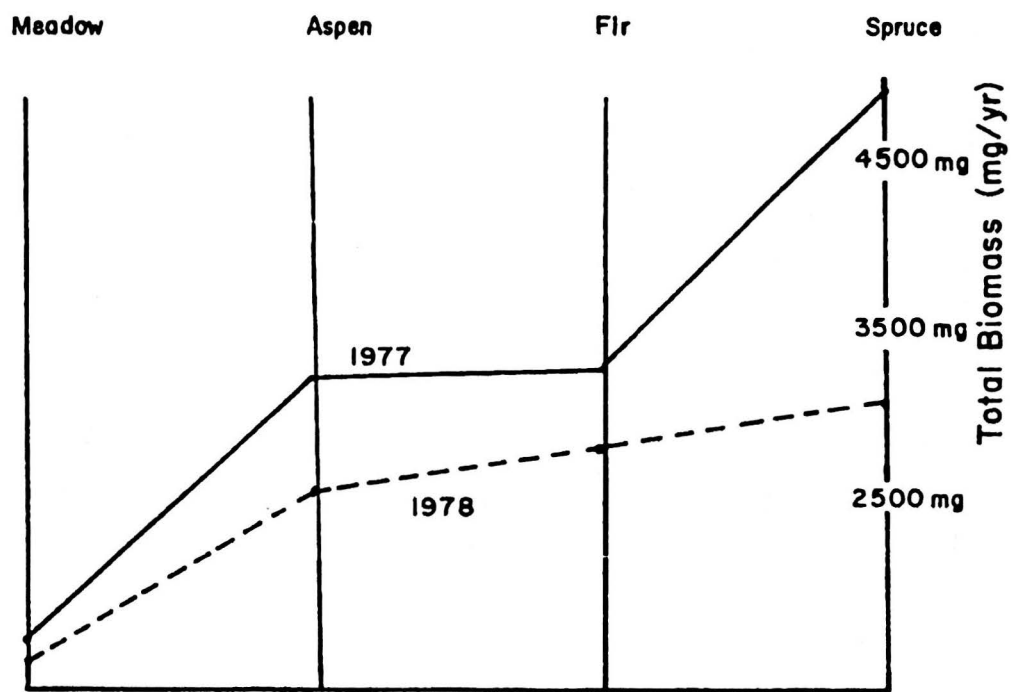


Fig. 30. Top, relative proportions of hunting spiders (active hunters plus ambushers) versus web-spiders in 4 ground strata communities of spruce-fir sere for 1977 and 1978. Bottom, relative proportions of annual versus semi-annual and biennial spider species in 4 ground strata communities of a spruce-fir sere for 1977 and 1978.

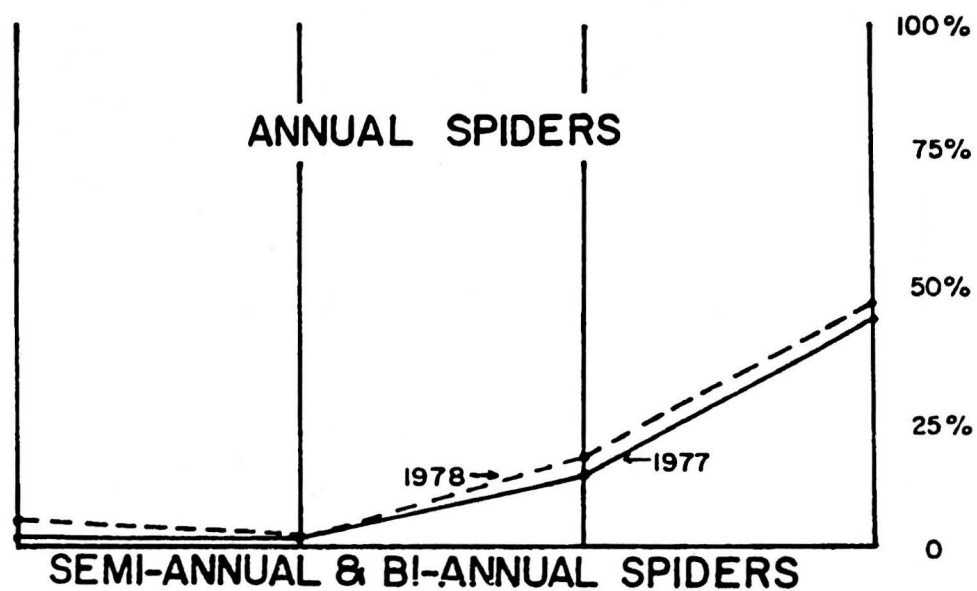
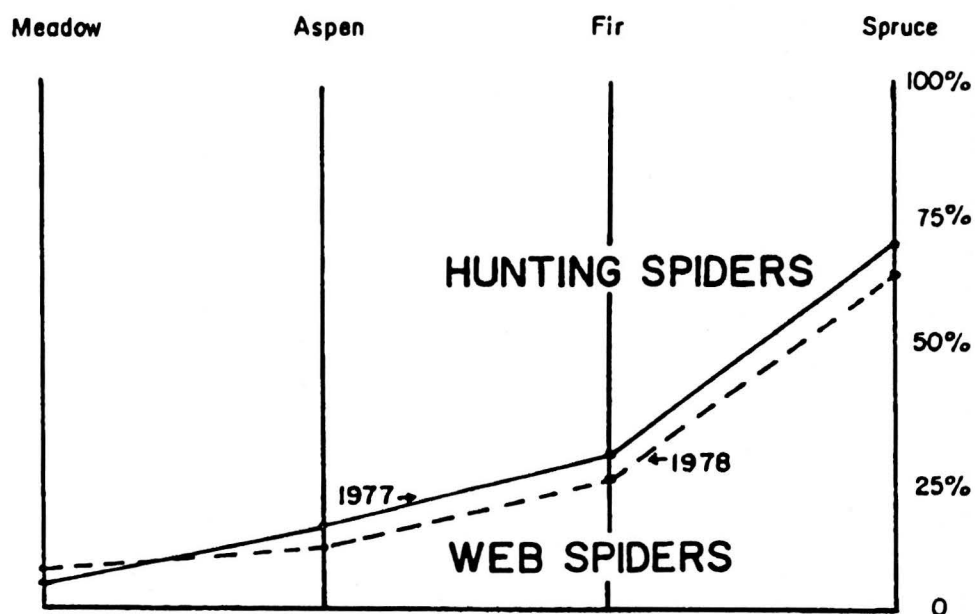
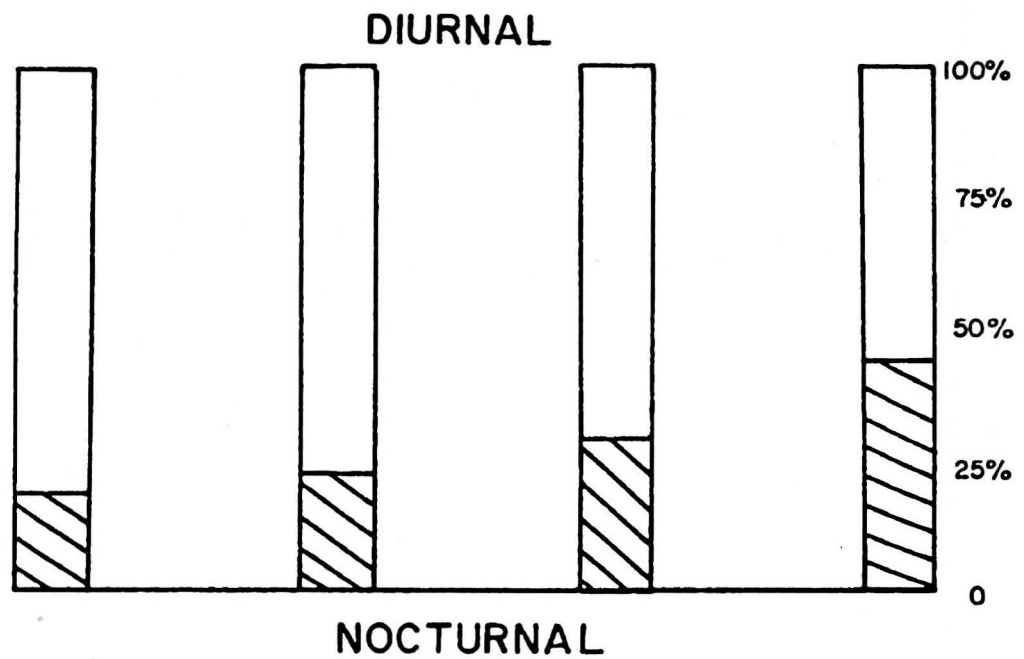
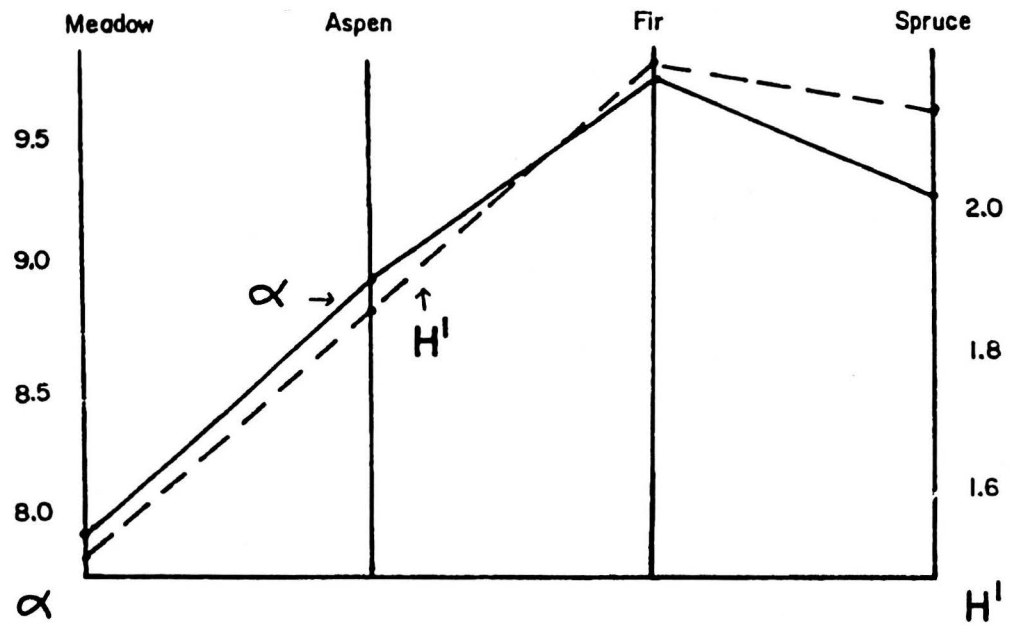


Fig. 31. Top, values for 2 species diversity indices in 4 ground-strata spider communities of a spruce-fir sere. Bottom, relative proportions of diurnal and nocturnal hunting spiders (active hunters plus ambushers,) in 4 ground-strata spider communities of a spruce-fir sere.



## DISCUSSION

The communities

Five spider communities were operationally defined. The communities and the number of resident species are: meadow (13), aspen (18), fir (19), and spruce (16) ground stratum spider communities (hereafter referred to as "meadow," "aspen," "fir," and "spruce" communities), and a single conifer tree stratum spider community (16) (hereafter referred to as "tree" community). Since there was little overlap of spider species between the tree and ground stratum communities (adults of only one species, T1, Steatoda hespera, of the 44 resident species of the sere were considered residents in a ground stratum community, spruce, and the tree stratum community) (Fig. 15), these communities will be discussed separately.

The greatest difference among ground-dwelling spiders of the study plots is between meadow and forest (Figs. 6-7). The meadow community had the fewest resident species but the highest ratio of characteristic to resident species ( $0.69$  where  $S_C/S_R = 9/13$ ). Species are defined as characteristic of the community in which they are maximally abundant. Adapting to the meadow habitat and having the necessary attributes to occur in the forests may not be compatible. The meadows, because of their dramatic diurnal temperature fluctuations and the low humidity, seem to be the abiotically most severe environments. In such an environment physiological constraints are important.

While my stands represent 3 forest types (aspen, spruce, and fir) only 2 spider faunas, aspen and spruce, can be distinguished. The third forest type, fir, is intermediate in its fauna and thus is occupied by an admixture of spruce and aspen spiders (Figs. 12-14).

Aspen and fir plots are more similar (Figs. 6-7) than any of the



other pairwise combinations of plots. Thus, although different trees are present in the 2 habitats the spider communities of the ground stratum are similar. Spiders of the coniferous forest ground stratum communities seem to be associated with structural or physiognomic factors rather than with either of the conifer tree species per se. One plot (S1) which to my eye is physiognomically fir-like, clustered with the representative fir plots, although spruce predominated (Appendix I). Similarly, a spruce-like fir plot (F3), was inhabited by a spider fauna similar to that of normal spruce plots (Figs. 6-7).

The meadow and spruce stages exist at polar extremes on a habitat gradient the similarity of the community types is 0.38 for the meadow and 0.45 for the spruce, the similarity coefficient of the aspen-fir assemblage is 0.61 (Fig. 6).

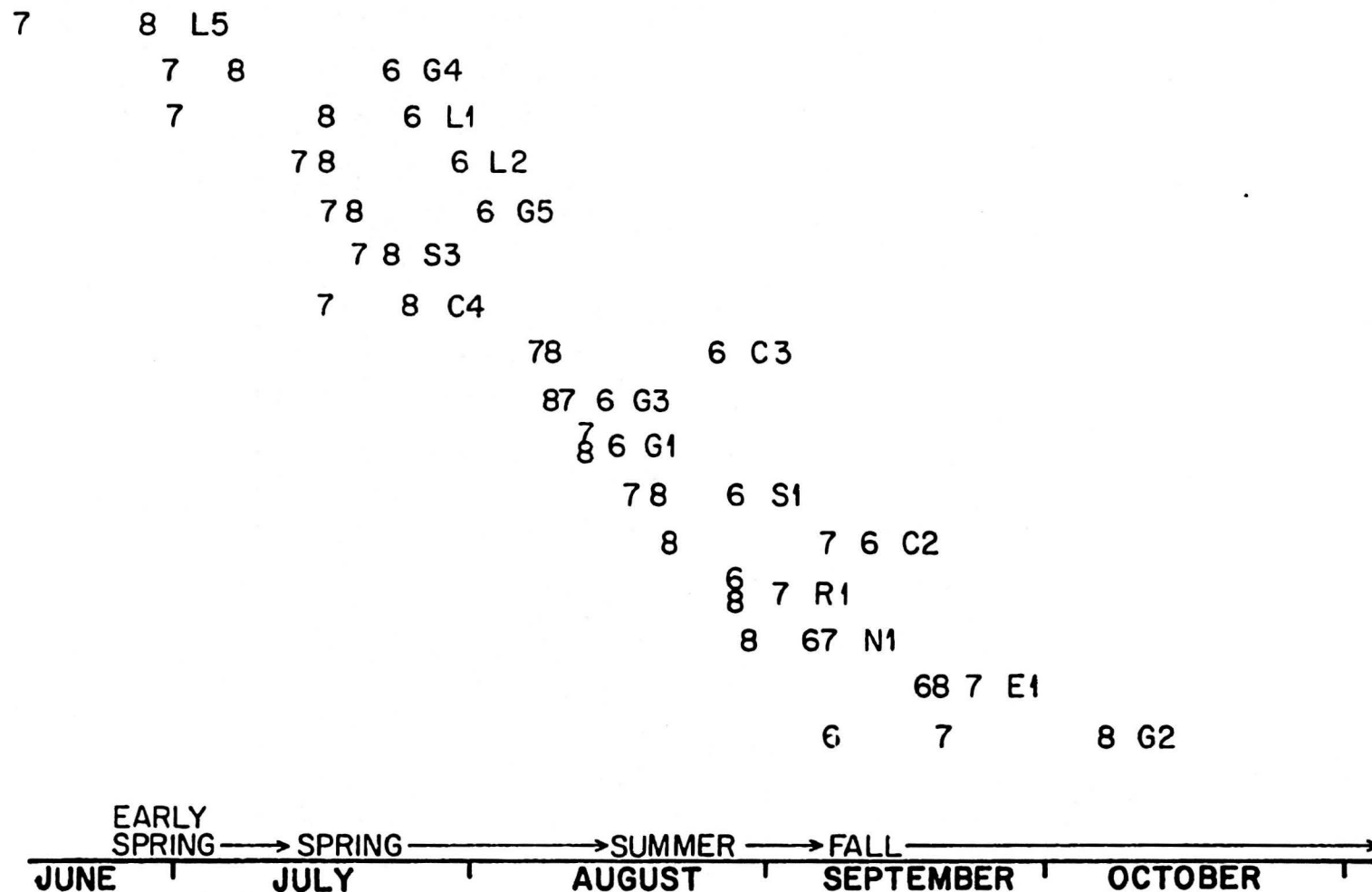
The ground stratum communities were phenologically similar, although a spring biomass peak was lacking in the meadow (Fig. 27). The year-to-year variation in seasonal activity, measured on an absolute (i.e., Julian calendar) scale was not considered to be significant. A spider species is active during the same season every year (Fig. 32).

There was no discernible difference between the spider populations occupying the tree strata of the 2 conifer species (Fig. 8). Stratton et al. (1979) found that different spider communities occupied the 3 conifer taxa which were considered to be physiognomically different at a site in northern Minnesota. I hypothesize that the fir and spruce trees of the School Forest are so physiognomically similar that spiders do not distinguish between them.

#### Spider guilds

A recent interest in the functional aspects of community components

Fig. 32. Date of mean activity of males of 16 ground-dwelling spider species, 6 = 1976, 7 = 1977, 8 = 1978. For species code designations, see Table 4.



is characterized by the introduction of the term guild. Root (1967) defined guild as "...a group of species that exploit the same class of resources in a similar way." This definition has 2 implications. First, one must clearly define what is meant by "same class of resources." Secondly, one must define what is meant by resource exploitation in a "similar way."

Arachnologists to date either implicitly or explicitly divided spiders into guilds based on the manner of obtaining prey. In 2 of the earlier synoptic collations of spider natural history and taxonomy (Comstock, 1912; Emerton, 1902), the 2 "groups of families" listed by Emerton--web-spiders and wandering spiders--have been recognized numerous times (e.g., Balogh and Loska, 1948; Heydemann, 1961; Juberthie, 1955; Petrusiewicz, 1938, in Turnbull, 1973), as have 3 of the 4 groups--web-spiders, ambushers, hunters, and kleptoparasites--listed by Comstock (1912). Kleptoparasites have seldom (but see Lubin, 1978; and Robinson and Robinson, 1970). been allotted separate foraging strategy status. Web-spiders, ambushers, and hunters have often been considered to employ discrete foraging strategies (e.g., Huhta, 1971; Lowrie, 1942; Luczak, 1963; Stratton et al., 1979). To the best of my knowledge, all workers who have considered the matter have differentiated web-builders from non-web-builders. The criterion for that distinction seems to be that web-builders catch prey in a semi-permanent web, whereas non-web-builders do not use a web when foraging, or use it differently.

Whether a spider is an ambusher or a hunter is objectively determined, by its behavior. Spiders which wait motionlessly and pounce on prey are ambushers; those which actively search for prey are hunters.

Gertsch (1949) apparently employed the usual criterion of web-versus

non-web-builder, and another criterion for vagrant spiders related to their use of vision when hunting, such that he recognized web-builders, long-sighted vagrants and short-sighted vagrants. Like other workers Barnes (1953) categorized spiders into 3 groups--web-builders and hunters of herbaceous stratum, cursorial spiders of the ground stratum, secretive forms of the leaf-mold--using vertical location as one criterion and behavioral propensities as the other. The foregoing are examples of the large number of different 3-group systems which could be described by using different criteria.

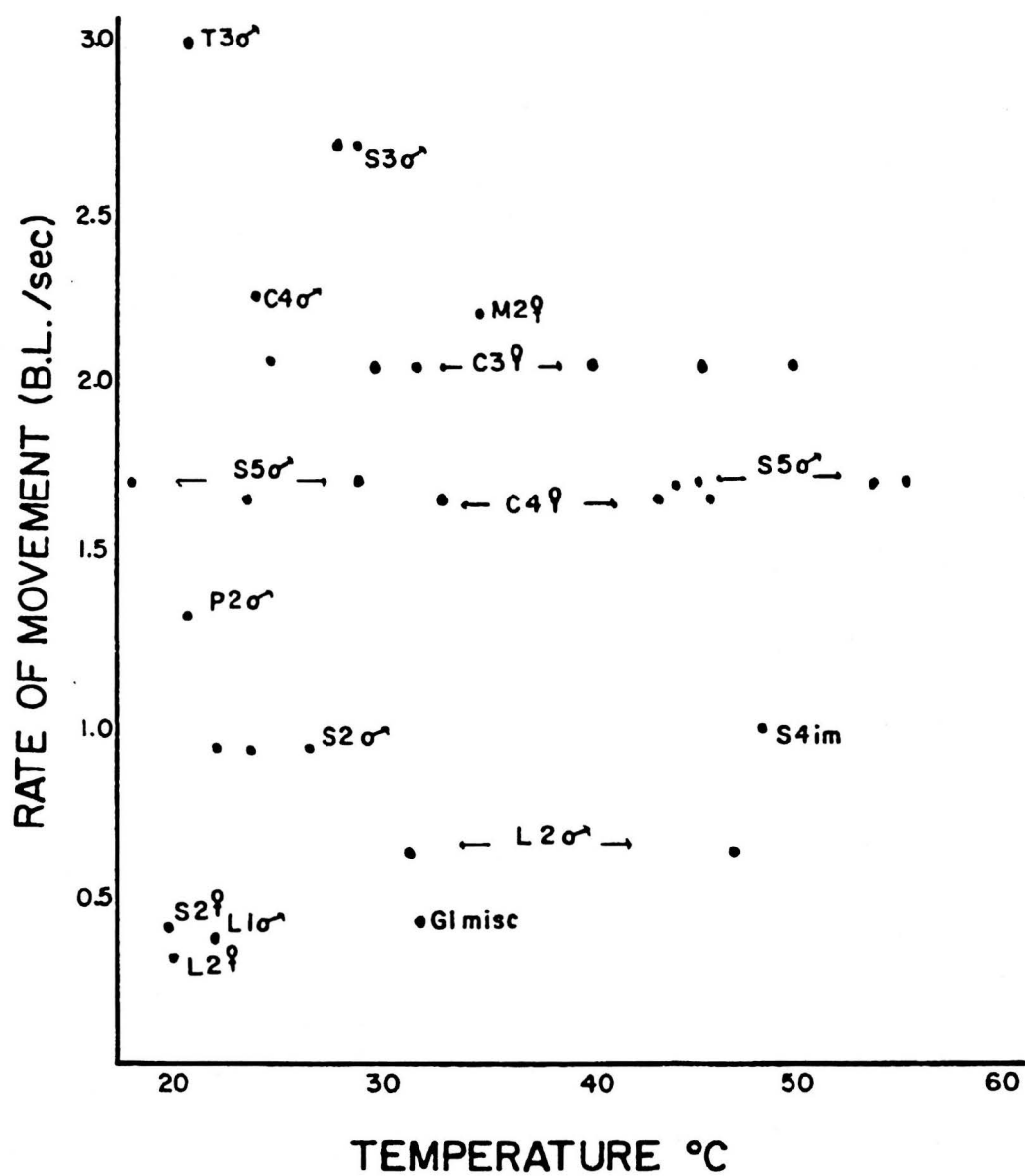
Arachnologists who have differentiated hunters and ambushers have usually done it along strict taxonomic lines at the family level. There is little agreement about which families are to be included in which categories. Thus, Breymeyer (1966) included agelenids, hahniids, lycosids, pisaurids, and thomisids in the wandering spider group; whereas the wandering spider "syntrophium" of Balogh and Loska (1948) consisted of hahniids, ctenids, and pisaurids. Turnbull (1973) considered ambushers and hunters to represent extremes of a continuum from, respectively, thomisids to clubionids, with pisaurids, philodromids, lycosids, salticids, and gnaphosids connecting them in that order.

The problem has been exacerbated in recent years when workers have intentionally attempted to consider both the resource class and the foraging strategy conditions when defining criteria to use for guild categories. Thus Abraham (1979) recognized 3, 5, or 7 guilds, Enders (1976) recognized 8 but implied that there are many more, Hatley (1978) recognized 8 guilds (not the same ones that Enders listed), Post and Riechert (1977) recognized 11 guilds, and Robinson (1978) analyzed the interactions among 4 guilds. Lubin (1979) listed 5 web-builder guilds,

differentiated on the basis of web shape.

Although the guild is an ecological category of convenience, arachnologists seem to accept the same criterion for hunting-ambushing spiders, but they apply it idiosyncratically. There is evidence that the criteria--ambushers wait for prey, hunters search actively--can be quantified. Carrel and Heathcote (1976) described 5 "separate foraging styles" when they compared heart rate and body weight of spiders: 1) large hunters (lower Standard Metabolic Rate, SMR, than expected); 2) web-weavers (higher SMR than expected); 3) small hunters; 4) tarantulas; 5) primitive hunters and weavers. The last 2 named are not relevant to this discussion. Enders (1976) has argued, primarily on theoretical grounds, that large spiders must be ambushers because of "freight" cost restrictions. My time-budget data indicate that neither family affiliation (excepting that the species of some families, e.g., clubionids, are usually small, whereas the species of other families, e.g., lycosids, are usually larger) nor temperature (Fig. 32) are significantly related to the foraging rate of active hunters. It must be noted that time-budget data were recorded for active spiders. They were probably thermoregulating behaviorally; and thus the body temperatures of the spiders and ambient temperatures were probably different. Body size was significantly correlated to foraging rate and the upper limit for active hunters (x-intercept, Fig. 6) corresponds to the lower limit of body size for Carrel and Heathcote's "large hunters." There are, then, 2 reasonable criteria for ambushers and hunters: 1) family affiliation, such that the species of some families, thomisids and philodromids for example, are ambushers; 2) body size, such that spiders with a body length (B.L.)  $> 3\text{mm}$  are ambushers, smaller spiders, not of ambushing families, are active hunters.

Fig. 33. Plot of rate of movement against ambient temperature  
for 14 hunting spider species.





Three levels of ecological categorization are proposed. Web-builders and non-web-builders are the 2 groups of the coarsest level of distinction. Ambushers, hunters and web-builders are 3 reasonably separate foraging strategies. And the 9 "guilds" presented in Table 3 are what I consider the finest degree of partitioning which is consonant with usefulness.

Guilds of ambushing and hunting spiders are based on the reasonable evidence that non-web-builders exhibit diel activity patterns (Dondale et al., 1972; Gertsch and Riechert, 1976; personal observation) and it is assumed that different prey also are active at different periods of the day. There is some indication that web-builders catch significantly different portions of the prey spectrum depending on what kind of web they build (Turnbull, 1973), and so I have used a minor modification of the web-shape criteria proposed by Lubin (1979) for web-builder guilds. Most webs are semi-permanent and there is some indication that at least some web-builders do not exhibit diel activity, but will accept prey at any time (Williams, 1962).

#### Physical factors

The distributions of spider species which use different foraging strategies (Fig. 16) and spider species of the ground stratum communities (Figs. 17-18) are canonically correlated to three environmental factors. The meadow factor (M.F.) consists of one environmental variable (bare dirt); the aspen factor (A.F.) consists of 2 variables (grasses and forbs, low foliage index); and the spruce factor (S.F.) consists of five associated variables (litter depth, tree basal area, canopy cover, dead leaves, and needles, logs) (Table 6).

In a few instances, there is empirical evidence to suggest a possible cause-effect relationship represented by these canonical correlations. Across the sere there are 7 resident erigonids (unidentified, see Table 4); of these, 4 are characteristic of spruce, 1 of fir, and 2 are aspen spiders (Figs. 12-14). The 2 species which build webs among the bases of grass stalks are aspen spiders; those which build webs in litter are characteristic of spruce. Since the A.F. variables are low foliage and the "best" (i.e., highest loading, Fig. 18) S.F. variable is litter depth, it is reasonable to posit a possible cause-effect relationship between aspen and spruce factors and the characteristic aspen and spruce erigonids.

The distribution of Callobius nomeus and the S.F. are highly correlated (Fig. 18, right). C. nomeus is the predominant spruce spider, it builds a web in aspen, fir, or spruce habitats in litter of sufficient depth (Fig. 24).

The most abundant species of the sere was Pardosa mackenziana, a lycosid which was characteristic of aspen, and whose distribution was correlated to the A.F. (Fig. 17, right). In Colorado P. mackenziana "frequents shrubby areas" (Schmoller, 1970). If I assumed a cause-effect relationship for the A.F. and the distribution of P. mackenziana, I would expect it to occur on the ground among shrubs where Schmoller found it.

Whether the observed relationships between spider distributions and environmental factors are cause-effect or not could, of course, only be determined by setting up an hypothesis, and performing experimental manipulation of the environmental variables to test it.

The more substantial value of the correlations is the use which can be made of the quantifiable environmental variables as

predictive indices of spider community composition. Whether a cause-effect relationship exists or not is a moot point. Nor is it necessary to assume that the spider species are actively responding to specific environmental variables and so selecting the habitats which they will occupy.

#### Community structure

The structures of the spider communities of the study site are described as the distribution of spider species in 6 dimensions of a hyper-space. Two of the dimensions are related to food (type and size), 2 are related to phenology (seasonal and daily), and 2 are spatial (habitat and microhabitat).

Two of the important ecological processes which mediate the location of a species in the multi-dimensional framework of a community are physical factors and competitive interactions. If any of the tolerance limits of a species are violated by the environmental conditions in a habitat, either biotic or abiotic in nature, the species will be excluded. The exact position which a species occupies in a habitat will be determined or modified, at least in part, by its encounters with other species which require the same limiting resources.

Size and foraging technique attributes and patterns of occurrence in time by the resident spider species of a habitat represent the structures of those communities (Figs. 19-23). The patterns of microhabitat occupancy by those species (Figs. 24-25 ; Tables 7-8) are additional structural components.

The structural patterns of food use in time and space by different species of a community result from long term co-adaptation by the

component species. The community characteristics of any species are the result of evolutionary and ecological processes occurring at various time scales. In one sense, since a species always occurs in a milieu with other species, we can say that all of these species are part of its evolutionary context, i.e., all the species in an ecosystem are to some extent involved (Whittaker and Woodwell, 1972). In a few instances for the spiders in this study the nature of the original axis of overlap for a pair of species can be inferred. I have chosen 4 pairs of similar-sized species for which the axis of probable differentiation can be isolated (Fig. 25). For 2 species a linear dimension (i.e., body length) ratio of the larger to the smaller of 1.28 or greater is sufficient for ecological segregation by size (Hutchinson, 1959). It is assumed that food, time, and space, are the important resources which are partitioned (Schoener, 1974).

Arctosa alpigena and Pardosa mackenziana are large (B.L. ratio = 1.09) forest-dwelling lycosid spiders which are active in the spring (Fig. 22) and forage (Fig. 25) in similar microhabitats. Of the variables which I have studied A. alpigena and P. mackenziana differ only in that A. alpigena is nocturnal and P. mackenziana is diurnal.

The medium-sized (B.L. ratio = 1.03) clubionid ant mimics, Micaria "A:" and Micaria "B," are functional equivalents in different habitats. They hunt actively during the day in similar microhabitats (Fig. 25) in the spring (Figs. 19-20). Micaria "A" is a forest spider, whereas Micaria "B" is characteristic of the meadow. In the communities where they are residents they occupy similar positions along the axes for which I have data.

Two large (B.L. ratio = 1.12) meadow spiders, the gnaphosid Zelotes tuobus and the salticid Pellenes americanus, are diurnal,

summer-active, hunters (Fig. 19). These 2 spiders forage in different microhabitats (Fig. 25); P. americanus forages on the surface, Z. tuobus presumably forages below the surface. (Time of occurrence below the surface was calculated when a spider was observed periodically entering and leaving the microhabitat.) They appear to utilize the same portions of 5 resource axes; it is inferred that they coexist by virtue of their segregation on the microhabitat axis.

The interpretation of the nature of the interaction between Pellenes laggani and Metaphidippus aeneolus seems to be complex. These large (B.L. ratio = 1.00) salticids are diurnal hunters which are spring-breeding, forest species. M. aeneolus hunts in the tree stratum, whereas P. laggani does not venture higher than 15 cm from the ground surface. Having observed both species in the field, they appear to behave similarly, i.e., do the same thing in different strata, and in that sense are functional equivalents.

The 2 lycosids coexist spatially in the forest habitat because they are separated along the daily temporal axis. Z. tuobus and P. americanus coexist spatially in the meadow by virtue of differential microhabitat use. The 2 clubionids do not coexist spatially. I infer that their separation may have resulted from their previously having interacted competitively. Competitive exclusion is also inferred for the pair of salticids.

There are a large number of possible pair-wise interactions between the resident species of the 5 seral communities; 4 pairs of species were selected for which a single axis of probable differentiation could be isolated. At a higher level of abstraction, however, the species of different communities can exhibit resource partitioning in different

dimensions to varying degrees. For example, invertebrates are expected to be segregated in seasonal and daily times of activity, and herbivores are not expected to be separated in time because the food which they exploit is not active at different times, and because habitat dimensions are usually more important than food-type or temporal dimensions (Schoener, 1974).

Dominance-diversity curves (Figs. 10, 15) are thought to provide insight into the manner whereby species apportion resources (May, 1975). None of the dominance-diversity curves fit the log-series model at the 95% level ( $\alpha = 0.05$ ), at the 90% level ( $\alpha = 0.01$ ) the dominance-diversity curves of the 3 forest ground stratum communities fit the log-series model (Fig. 9). Although one cannot statistically test the fit of the dominance-diversity curve to a geometric model, it appears that the dominance-diversity curves for the meadow and tree communities are approximately geometric. The geometric nature of the dominance-diversity curve of a community is indicative of "relatively small and simple communities of species, whose ecology is governed by some dominant factor...." (May, 1975). Most (88.6%, Fig. 5) of the meadow spiders are diurnal hunters. So, little differentiation is present in the daily time and food-type dimensions. And since the meadow, lacking trees, is less heterogeneous spatially than the forests, the degree of microhabitat separation is probably limited. The "dominant factor," then, is presumably differential use of food-sizes over seasonal time (Fig. 19).

Spiders of the tree community lack temporal stratification. Thirteen of the 15 species which breed there do so during the spring (Fig. 23); and 14 of the 15 build webs which function throughout the day. Differential use of the architectural structure of the forests is probably the primary

way tree spiders are segregated (Fig. 24).

The log-series dominance-diversity curve of the spruce spiders (Fig. 9) may reflect the existence of "many" (i.e., spatial and temporal) important ecological factors. The resident spiders of the spruce community are dispersed in seasonal (Fig. 23) and daily time (Fig. 31, bottom; 44% of the spruce spiders are nocturnal). They use different foraging strategies (Fig. 30, top; 69 % of the spruce spiders are web-spiders) in the complex (Uetz, 1977) deep-litter (Table 6) forest floor.

#### Ecological succession

The communities of a successional sere are a chronosequence from young to old. Thus, parameter values of young communities can be compared to the values of older communities to describe community changes over time. I will attempt to relate the changes observed in spider communities to general successional trends. Odum's (1969) codification of predictions relating to the nature and direction of successional changes in various community parameters can serve as the model to which observed changes can be compared.

Total organic matter is hypothesized (Odum, 1969) to be greater in more mature stages. The total biomass of spiders increased monotonically from meadow to spruce stages (Fig. 29, top). The active density units of spider pitfall trap data are probably not comparable to absolute density (see Materials and Methods). Making the, probably invalid, assumption that both measures are comparable, I provisionally accept Odum's organic matter hypothesis.

Two of Odum's hypotheses concern the number and distribution of species. He hypothesized that the number of species increases with community maturity as does the equitability component of species diversity. Both trends were observed. Number of species (49) and number of resident species (19) increased to a maximum in the fir stage (Table 5,  $S_T$ ,  $S_R$ ). Equitability of species was highest in the mature conifer stages (Table 5,  $J' = 1.7$ ). The same trends were observed for Fisher's Diversity Index and the Shannon-Wiener Diversity Index (Table 5,  $\alpha$ ,  $H'$ ; Fig. 31, top); like species richness, diversity peaked in the fir ( $\alpha = 9.35$ ,  $H' = 2.45$  for all species, 2.17 for resident species). Guild diversity increased monotonically to a maximum in the spruce (Table 5,  $H' = 1.42$ ). Odum's species diversity hypotheses are not rejected on the basis of spider community data.

Stratification and spatial heterogeneity are predicted to change from a poorly-organized to a well-organized state (Odum, 1969). The proportion of web-spiders increases in more mature communities (Fig. 30, top). Since the web is a semi-permanent structural device which usurps space it also increases spatial heterogeneity. Spider communities of 2 strata (ground and tree) were present in the mature stages. On the basis of the evidence presented I do not reject Odum's stratification and spatial heterogeneity hypothesis.

Organism size is hypothesized to increase with maturity (Odum, 1969). The average size of adult spiders does increase monotonically from meadow to spruce (Fig. 29, bottom). However, the largest spiders of the sere were Antrodiaetus montanus and Alopecosa kochi (Table 4), both characteristic meadow spiders. Depending on which criteria are used--average size or maximum size--one could either accept or reject



the organism size hypothesis. Assuming that the average size is more meaningful, I do not reject Odum's organism size hypothesis.

Life cycles are hypothesized to be short and simple in developmental stages and long and complex in mature stages (Odum, 1969). The proportion of semi-annual species increased with maturity (Fig. 30, bottom). They are small spiders with 2 generations per year, so they have the shortest life cycles of the seral spiders. The proportion of biannual species also increases with maturity (Fig. 30, bottom). So, the proportion of species with either short or long life cycles increases in more mature stages. There were more annual spiders in the earlier stages. If the annual life cycle is interpreted to be simpler than either the semi-annual or the biannual, then one could argue that the simple-complex aspect of the life cycle hypothesis is supported by the spider community data. There is, however, no acceptable definition for complex (May, 1976), and so neither aspect of the life cycle hypothesis can be rigorously tested.

Dondale et al. (1972) proposed that temporal stratification is maximum (i.e., 50% diurnal, 50% nocturnal species) in "climax" communities. The amount of temporal stratification was approaching the maximum in the spruce community (Fig. 31, bottom). The temporal stratification hypothesis is provisionally accepted.

In summary, 6 of Odum's (1969) hypotheses were addressed; 5 of the 6 were provisionally accepted, the life cycle hypothesis could not be tested. One hypothesis proposed by Dondale et al. (1972) was provisionally accepted.

## SUMMARY AND CONCLUSIONS

Of the 99 spider species which were collected during the course of this study, 44 were considered residents of the sere; the residents were distributed among 5 nominal communities, including: meadow, aspen, fir, and spruce ground strata spider communities, and one conifer tree-stratum community. Among the ground-stratum communities those at the successional extremes--meadow and spruce--were the most distinct. Among the forest communities only aspen and spruce communities were distinct. The fir spider community is faunally intermediate between aspen and spruce, i.e., contains an admixture of aspen and spruce spiders. The fir and spruce ground-stratum spider species are associated with habitat physiognomy rather than with the tree taxa per se. The spider faunas occupying the tree-stratum of the fir and spruce stages do not differ.

Criteria for recognizing 3 foraging strategies and 9 spider guilds are presented. The 3 foraging strategies are web-building, ambushing, and hunting. Web-building spiders inhabit a web when foraging. Ambushing spiders wait for prey, while hunting spiders actively search for prey. Large spiders (i.e., body length (B.L.)  $> 8$  mm) are ambushers. Hunting spiders are small (i.e., B. L.  $< 8$  mm). Spiders using the same foraging strategies, but exploiting different resource classes are considered to belong to different guilds. Web-building guild criteria are web shapes, the 5 guilds include: line-, surface-covering-, orb-, sheet-, and space-webs. Guilds of ambushing and hunting strategies are based on time of activity and include diurnal and nocturnal ambushing and hunting spiders.

The distribution of hunting spiders was positively correlated canonically to meadow and aspen environmental factors. The meadow factor consists of the single environmental variable, bare dirt; the aspen factor consists of 2 environmental variables, grasses and forbs, and a low foliage index. Web-spiders and ambushing spiders are positively correlated canonically to a spruce factor, which consists of the 5 environmental variables, litter depth, canopy cover, tree basal area, dead leaves and needles, and logs. Distributions of characteristic spider species of the meadow, aspen, and spruce ground-stratum communities were positively correlated canonically to the meadow, aspen, and spruce environmental factors, respectively. Evidence was considered adequate for postulating a cause-effect relationship between the aspen and spruce factors and 8 of the resident spider species. Two unidentified erigonid species and the lycosid, Pardosa mackenziana, were associated with the aspen factor; 4 unidentified erigonid species and the amaurobiid Callobius nomeus, were associated with the spruce factor.

The structures of the 5 nominal communities of the sere are represented in 6 dimensions, including: 2 spatial dimensions (habitat and microhabitat); 2 temporal dimensions (daily and seasonal), and 2 food-related dimensions (food-type and food-size). The axes of probable differentiation were isolated for 4 pairs of species. The lycosids Pardosa mackenziana and Arctosa alpigena differ in daily time of activity; the meadow spiders Zelotes tuobus and Pellenes americanus forage in different microhabitats; the clubionid ant mimics Micarria "A" and Micarria "B", and the forest salticids Pellenes laggani and Metaphidippus aeneolus, are functional equivalents in different habitats.

The dominance-diversity curves of the meadow ground-stratum spider community and the conifer tree-stratum spider community are geometric. The "dominant factor" which governs the ecology of the meadow spiders is differential use of the habitat through seasonal time; exploitation of different food-sizes is probably a factor of secondary importance. The dominant factor for the tree spider community is differential use of the microhabitats provided by the architectural structure of trees. The species distributions of the forest ground-stratum communities are log-series. There is no primary factor to which those forest spiders respond; both spatial and temporal resource dimensions are important.

Six of the hypotheses about successional change in animal community characteristics posited by Odum (1969), and one hypothesis proposed by Dondale et al. (1972) were addressed. Increases with maturity predicted by Odum were observed for the following spider community parameters: total biomass, species diversity--richness component, species diversity--equitability component, stratification and spatial heterogeneity, and organism's mean size. The increase in temporal stratification predicted by Dondale et al. was observed. Odum's life cycle hypothesis (i.e., short and simple life cycles in early stages, long and complex ones in mature stages) could not be tested because, depending on the life cycle type considered, I found diametrically opposed trends (semi-annual and biennial life cycle types both increased with maturity). If either trend were chosen the life-cycle length aspect of the hypothesis could either be accepted or rejected. The second aspect of the hypothesis could not be addressed because it is not clear how the terms "simple" and "complex" can be applied to spider life cycles.

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## APPENDICES

Appendix I. Statistical parameters for tree species in 9 forest plots of a spruce-fir sere: N = number of individuals;  $\bar{x}$  = average area (cm<sup>2</sup>) breast-height; S.D. = standard deviation of area at breast-height;  $\Sigma$  = summation of areas at breast-height; L = live; D = dead.

	Aspen		Fir		Spruce		Total
	L	D	L	D	L	D	
Plot A1							
n	79	8			2		89
$\bar{x}$	231.05	79.64			22.97		
S.D.	170.31	91.14			10.54		
$\Sigma$	18252.95	178.78			45.94		18936.02
Plot A2							
n	103	38	1		1		143
$\bar{x}$	110.28	14.55	62.07		12.97		
S.D.	149.60	15.34					
$\Sigma$	11358.86	552.95	62.07		12.97		11986.85
Plot A3							
n	170	19	8				197
$\bar{x}$	118.17	20.97	235.31				
S.D.	142.79	34.22	255.27				
$\Sigma$	20088.54	398.41	1882.46				22369.41
Plot F1							
n	1		117	16	37	3	174
$\bar{x}$	241.24		100.33	28.36	214.33	59.91	
S.D.			138.52	43.33	399.44	27.42	
$\Sigma$	241.24		8728.34	453.75	7930.13	179.73	17533.19

## Appendix I. Continued

	Aspen		Fir		Spruce		Total
	L	D	L	D	L	D	
Plot F2							
n	4	2	72	12	3		93
$\bar{x}$	697.39	388.57	176.60	611.62	825.85		
S.D.	561.76	43.89	297.05	586.05	653.47		
$\Sigma$	2789.57	777.13	12715.46	7339.44	2477.56		23309.59
Plot F3							
n	4	2	91	19	30	1	147
$\bar{x}$	779.18	216.67	295.82	363.23	706.31	447.73	
S.D.	314.80	223.57	431.00	580.17	1015.82		
$\Sigma$	3114.70	433.34	26919.41	6901.34	21189.18	447.73	59007.70
Plot S1							
n			17	6	40	5	68
$\bar{x}$			13.72	349.71	753.44	965.97	
S.D.			17.84	267.33	1107.90	1398.31	
$\Sigma$			233.25	2098.24	30137.48	4829.85	37298.82
Plot S2							
n		1	9	3	59	3	74
$\bar{x}$		324.29	299.85	905.47	657.88	93.81	
S.D.			470.60	393.16	542.23	64.11	
$\Sigma$		324.29	2698.66	2716.40	38815.10	281.43	44835.88

## Appendix I. Continued

Aspen		Fir		Spruce		Total
L	D	L	D	L	D	
Plot S3						
n	1	16	16	112	3	148
$\bar{x}$	585.56	158.89	110.78	465.37	60.74	
S.D.		214.29	160.45	483.46	59.83	
$\Sigma$	585.56	2542.24	1772.49	52121.95	182.21	54662.2



Appendix II.     Web measurement methodology

Three measurements were made on each web including: height; horizontal location in tree canopy; and size. Spiders which build line-, surface-covering-, or space-webs usually use a retreat, sheet-web spiders wait near the center of the web. The location of a retreat or the center of a sheet-web was taken as the point for determining the values for height and horizontal position. For orb-webs the center of the orb was the point so used.

Horizontal position for a web is determined as the ratio of the distance from tree trunk to web-center, divided by the distance from tree trunk to canopy edge. That value (as the average of n measurements) multiplied by 100 is the "index of peripherality" of Table 8. Orb-webs and sheet-webs between trees or built in litter on the ground were not considered to be in the canopy.

Web size was considered to be the length of a line-web, diameter of the orb of an orb-web, or maximum straight-line distance of sheet-, surface-covering-, or space web.

## CURRICULUM VITAE

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Born: 8 Dec. 1943 Birthplace: Salt Lake City, Utah

Height: 1.82 m (5' 11") Weight: 80.1 kg (176 lbs)

Marital Status: married, 14 July 1972, to Laurie Clair (Bonham)

Children: one

## EDUCATION AND DEGREES

Elementary and Secondary: public schools of Bountiful, Utah

## Undergraduate

University of Utah, 1962-63, 1964-65, 1968-69

Church College of Hawaii, 1963-64

## Graduate

University of Utah, 1969-72

Utah State University, 1975-79

## Degrees received

B.S. (Environmental Biology), University of Utah, 1969

M.S. (Biology-Herpetology), University of Utah, 1972

Thesis: Musk glands in Recent turtles.

Ph.D. (Biology-Ecology), Utah State University, 1979

Dissertation: Changes in spider community attributes  
along a subalpine successional gradient.

## POSITIONS HELD

Curatorial Assistant, Univ. of Utah Mus. of Zool. (Herpetology)

7/69-9/69. Performed curatorial duties associated with a large

(20,000+) working collection; prepared whole, shell and parts, cleared and stained, and skeletal specimens; took care of 100+ live specimens, mostly turtles.

9/70-12/70. Assisted in the design and implementation of a laboratory complex including a darkroom and a histology laboratory for basic research in herpetology.

Teaching Assistant, Department of Biology, Univ. of Utah

9/69-6/70, 9/70-6/71. Taught laboratories and lectured as required in elementary human anatomy, herpetology, and microtechnique.

Teaching Fellow, Department of Biology, Univ. of Utah

9/71-8/72. Laboratory Coordinator for an elementary human anatomy course with an enrollment of ca. 600 students and ten teaching assistants; wrote (with Dr. J. M. Legler) a 40-page Guide for Human Anatomy Teaching Assistants.

Genetics Lecturer (U.S. Peace Corps), Nat'l Univ. of Malaysia

12/72-2/75. Taught population genetics, general genetics, evolution, environmental pollution, general science (for 1st-year Moslem theology students), and 3rd-year seminar.

Faculty Adviser to Zoology Museum, Nat'l Univ. of Malaysia, 2/73-2/75.

Research Assistant, Ecology Center, Utah State University

6/76-9/76, 6/77-9/77, 6/78-9/78. Collected data for doctoral dissertation; assisted in supervision of technicians, and maintenance and operation of field station at which I resided.

Teaching Assistant, Dep't of Biology, Utah State University

9/76-6/77, 9/77-6/78, 9/78-6/79. Laboratory instructor in general biology, biology for the citizen, herpetology, animal communities, introductory physiology, human anatomy; cadavers were

used for the first time in human anatomy at Utah State during 1978 and 1979; I performed most of the dissection during 1978 and supervised six pre-medical seniors who dissected two cadavers during 1979.

#### HONORS AND AWARDS

National Merit Scholarship Letter of Commendation, 1962

Nominated to Sigma Xi, 1972

Graduate Research Fellowship, Utah State University, 1975

#### MEMBERSHIPS

American Arachnological Society

American Society of Ichthyologists and Herpetologists

American Society of Zoologists

Society of Systematic Zoology

The American Society of Naturalists

The Ecological Society of America

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#### EXTRACURRICULAR ACTIVITIES

8/65-1/68. Traveled and worked on the West Coast (U.S.A.), North Europe, the Balkans, West Asia Arab countries, Israel, and Quebec.

2/75-6/75. Traveled overland from Nepal to London, returning from Peace Corps assignment.

#### PAPERS IN PREPARATION

Spider biomass: correlation of dry weight to body length.

Plastral kinesis in Heosemys spinosa.

Musk glands in Recent turtles.

